

# GARDENING ANTS

## THE ATTINES



NEAL A. WEBER

## GARDENING ANTS THE ATTINES

ONE OF THE most remarkable of Nature's marvels is that of the gardening ants. These fascinating creatures, whose moundlike nests are a conspicuous feature of the landscape, in some parts of South America, raise their own food by planting and maintaining "gardens" of a tiny fungus that provides their whole diet. By their own excretions and physiological activities they fertilize their crop of fungi and keep it free from contamination by other organisms.

Professor Neal A. Weber of Swarthmore College presents in this book the results of thirty-seven years' study of these insects in their native haunts and in his laboratory. He describes, and illustrates by numerous pictures and maps, their behavior, their social organization, and their communications with each other by pheromones. His account of their gardens includes the life history of the specific fungus they have learned to cultivate as food.

This unusual book will appeal to general readers interested in animal life as well as to specialists. For the latter Professor Weber provides a full bibliography and a comprehensive index of scientific as well as popular names.

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The queen of a young Panamanian *Atta sexdens* colony and her polymorphic workers attending the early fungus garden. Her integument has been well licked by the workers.



# GARDENING ANTS, THE ATTINES

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# GARDENING ANTS THE ATTINES

NEAL A. WEBER

*Professor of Zoology, Swarthmore College*

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To  
JEAN, NANCY, JEFF and PETER





## PREFACE

My interest in ants arose early in life while watching mounds of a thatching ant on the prairie around my home in North Dakota. This ant later became the subject of my master's thesis at the University of North Dakota where the myrmecologist, Dr. George C. Wheeler, encouraged me to continue the study of ants. His major professor, William Morton Wheeler (no relation), became mine when I transferred to Harvard in 1932. While working on my assigned doctoral research on the holarctic ant genus *Myrmica*, I spent a summer in Cuba on a Harvard Travelling Fellowship and first became acquainted with the fungus-growing ants. The following year I was awarded a National Research Council Fellowship to study these ants at the Imperial College of Tropical Agriculture (now the University of the West Indies) in Trinidad. Since that time I have had numerous opportunities to observe and collect fungus-growing ants at many localities from their northern limit in New Jersey and California to their southern boundary in Patagonia.

I have studied gardening ants primarily to find out how they maintain a flourishing culture of one fungus in the continued presence of contaminant fungi. Though the various species display great morphological variety and are widely distributed throughout the New World, their behavior is fundamentally similar. To maintain this fungus, members of the colony lavish it with constant care and constant application of their excretions. It is not necessary for the ants consciously to weed out the alien organisms which flourish in their absence. Rather, this control is achieved through the behavioral pattern which causes the ant to apply its excretions to the fungus garden. These excretions turned out to be the key to the entire problem as I had long suggested. My chemist

colleagues further clarified this phenomenon by determining just what substances the excretions contain and which of these the ant fungus needs. During this long period of study the entire field of pheromone research developed and showed how the ants communicated with one another to maintain their colonies.

Truly the studies on the gardening ants have vividly illustrated how the pursuit of knowledge by many people with many points of view and different skills can converge to explain a fascinating example of mutualism between a plant and an animal. At the same time many new questions should occur to the reader to show that this field of study still challenges the skills and imagination of the scientific investigator.

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N. A. W.





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# GARDENING ANTS, THE ATTINES





# INTRODUCTION

Among about 10,000 species of ants there is one group of 180–200 species that differs from all the others by its habit of growing plants. The large species are notorious leaf-cutters, and attention has been concentrated on this aspect of their life to the neglect of fungus gardening which is a much more remarkable practice. The simple conclusion that gardening ants and their larvae feed on the pieces of leaves carried into the nests is incorrect. The leaf fragments are used for growing food in the form of a specific mold or fungus that luxuriates in the ant garden even though the ants are continually bringing in contaminants such as common soil fungi and bacteria on leaves and on their own bodies. These contaminants thrive in the same garden when the ants are removed. Only when the ants actually culture the garden does their own fungus grow so well. At first, the explanation of this phenomenon appeared to be that the ants weeded out other organisms. Later, it seemed that the ants produced some unusual antibiotic. However, this explanation is also unsatisfactory and an alternative explanation is developed in this book.

The evolution of a unique skill in fungus culturing has freed these ants from usual food limitations and has enabled them to expand in colony size. In the process a few species have developed some of the largest ant colonies known, with populations in the millions. To maintain such a colony they excavate a nest with many chambers in the soil and cut huge quantities of leaves for the gardens. The easiest plants to attack are often the same ones that man has planted for his own use. Other species of gardening ants are so small and inconspicuous that they are never seen unless looked for by the specialist, yet all of the species in this closely related group depend for survival on their own success as gardeners.

Besides their unusual gardening ability these ants show the general habits of ants that have always fascinated entomologists. They are all

social, living in colonies with a queen as the center of colony life and with workers to carry on the non-reproductive activities. Each colony rigorously excludes members of any other colony, whether of the same or of a different species, by means of a complex set of recognition signals. These ants communicate with one another by discrete chemicals, released by specific parts of the body, or by visual and tactile means. Their nests are highly plastic and are adapted by the ants to the environment. The ants partially control the environment by their engineering practices.

As the term is used here, gardening ants refers to all of the Attini or fungus-growing ants. The largest of these are the conspicuous leaf-cutters and belong primarily to the genera *Acromyrmex* and *Atta*, the former lacking a soldier type of worker and the latter possessing an extremely large form of the worker with disproportionately large head known as the soldier. These two leaf-cutters are so well known in each country as to have been given the colloquial names presented in chapter 1. They have by far the largest and most populous nests. Smaller gardening ants such as those of *Trachymyrmex* and *Sericomyrmex* are often inconspicuous leaf-cutters and are not often known to the layman.

The symbiotic association between the ants and their fungi is a mutualistic one, the association being essential to the survival of both organisms. The mutualism and the economic importance of the ants have attracted research by ecologists, biochemists, entomologists, mycologists, bacteriologists, botanists, agronomists, and animal behaviorists. The present account summarizes my observations on gardening ants during the past 37 years and the published research of numerous other workers. It is my hope that this book will serve as an introduction for students in these areas who may wish to fill any of the numerous gaps in our knowledge of the attine ants and their fungi.

# 1. THE RELATIONSHIPS OF GARDENING ANTS TO MAN

The leaf-cutting members of the attine ant tribe were a significant part of the fauna of the warm parts of the Americas even before the arrival of the American Indians. The Indians, as they proceeded south through Middle America and from one island to another in the Caribbean, encountered them on the semi-desert, the grasslands, at the margins of forests, and deep within tropical rain forests. First they met the ants in Mexico, where the women and especially the children with their observant eyes found the ants busily at work, cutting off the leaflets and flowers of *Acacia* and other plants and carrying them off to their nests. Such ants were merely a part of their world until someone discovered that they were good to eat.

## GARDENING ANTS AS FOOD

Locusts, termite queens, beetle larvae, and numerous other insects have been used as food by people throughout the world. Leaf-cutter ant queens of *Atta* have been eaten probably in all parts of their range, and *Acromyrmex* queens may be eaten occasionally. The queens are collected when they emerge by the thousands from colonies at times of mating and colony founding. Usually only the gaster (abdomen) is eaten since this is the tasty part filled with eggs and fat. The gasters are eaten either raw, roasted, or fried. In the United States in recent years *Atta* queens, fried and ready to eat, have been sold in cans, but it is likely that most of these have been bought primarily as conversation pieces rather than delicacies.

## LEAF-CUTTER ANTS AS ECONOMIC PESTS

An appreciation for flowers, evidently developed during the high civilization of Middle America, became associated with the leaf-cutters in mythology. *Popul Vuh* myths of Guatemala were described in French a century ago. In one tale, two young men were taken in ambush and required to bring four vases of flowers or forfeit their lives. During the night the captives called on the leaf-cutting ants, or zampopos, to bring the flowers. Guardians of the flower garden patrolled all night to prevent the captives from

getting the flowers. However, the ants worked all night unobserved, and according to the story, filled the vases with flower sections, and thus saved the men.

In spite of this tale the leaf-cutter ants have been generally considered by both Indians and subsequent human invaders of their habitat to be detrimental insects. Almost as soon as the Spanish arrived in the New World they published statements on the depredations of these ants. Bartolomé de las Casas in 1559 reported that ants destroyed cassia, orange, and pomegranate trees on Hispaniola. The nests were dug up and described as "white as snow." This was probably the first published record of the gray-white fungus gardens and brood of the smaller leaf-cutter (*Acromyrmex*).

Schomburgk (1840-1844) wrote an account of the natural resources of British Guiana (Guyana) in which he describes the effect of *Atta cephalotes* on the cassava plantations.

These terrible destroyers of the cassava and plantain fields have their dwellings underground and increase at such an enormous rate that their nests resemble huge mounds of thrown-up earth. . . . In a short while the ants eat away the whole of the leaves and drag them into their subterranean dwellings. If a field is once visited and robbed by them, the destruction of the whole is to be feared. Even when their nests are situated a quarter of an hour distant they will find the plantation and soon clear all the way up to it on one of the most busily occupied paths imaginable.

Although the fungus gardens had been seen hundreds of years earlier, there was considerable doubt about what the ants were doing with the leaves. Most persons still today assume the ants are eating the leaves, but Belt (1874) first corrected this view. His account of *Atta cephalotes* stated,

Notwithstanding that these ants are so common throughout tropical America, and have excited the attention of nearly every traveller, there still remains much doubt as to the use to which the leaves are put. Some naturalists have supposed that they use them directly as food; others, that they roof their underground nests with them. I believe the real use they make of them is as a manure, on which grows a minute species of fungus, on which they feed;—that they are, in reality, mushroom growers



and eaters. This explanation is so extraordinary and unexpected, that I may be permitted to enter somewhat at length on the facts that led me to adopt it. When I first began my warfare against the ants that attacked my garden, I dug down deeply into some of their nests. In our mining operations we also, on two occasions, carried our excavations from below up through very large formicariums, so that all their underground workings were exposed to observation. I found their nests below to consist of numerous rounded chambers, about as large as a man's head, connected together by tunnelled passages leading from one chamber to another. Notwithstanding that many columns of the ants were continually carrying in the cut leaves, I could never find any quantity of these in the burrows, and it was evident that they were used up in some way immediately they were brought in. The chambers were always about three parts filled with a speckled brown, flocculent, spongy-looking mass of a light and loosely connected substance. Throughout these masses were numerous ants belonging to the smallest division of the workers, and which do not engage in leaf-carrying. Along with them were pupae and larvae, not gathered together, but dispersed, apparently irregularly, throughout the flocculent mass. This mass, which I have called the ant-food, proved, on examination to be composed of minutely subdivided pieces of leaves, withered to a brown colour, and overgrown and lightly connected together by minute white fungus that ramified in every direction throughout it. . . . That they do not eat the leaves themselves I convinced myself; for I found leaves that had been exhausted as manure for the fungus, and were now left, and served as food for larvae of Staphylinidae and other beetles.

The success of the fungus-growers is due primarily to the ability of the fungi to grow on almost any kind of leaf or plant material that occurs everywhere. By nesting in soil the ants avoid many competitors, predators, and parasites and have a moist environment for the fungus. If the surface layers dry out, the ants excavate deeper.

Like some other successful animals, they adapt to human activities. The practice of growing crops is made to order for them since they can use leaves of most of man's crops with great success. Cocoa, coffee, and citrus leaves are easy for them to cut and, when they finish with one tree or bush, they merely move on to the next in the row.

The economic importance of the ants depends largely on the abundance of *Acromyrmex* and *Atta*. Nevertheless, the smallest and northernmost fungus-grower, *Trachymyrmex septentrionalis*, may cause United States truck gardeners to call their county agent. The usual damage is from ants going down rows of seedlings and

carrying each shoot back to their nests. *Atta texana* also kills many seedling pines in Louisiana.

The techniques applied by agriculturists in the United States to estimate monetary damage by specific pests have been applied to fungus-growing ants. The annual losses from these ants in both North and South America were estimated by Townsend in 1923 to be as much as one billion dollars. The loss in the state of São Paulo, Brazil, was estimated at ten million dollars annually in 1929. In Texas alone, the damage from *Atta texana* was estimated to be \$1,640,000 in 1936. The annual loss per nest was considered to be three to four dollars in cereal and forage crops and fifteen dollars or more when nests were in orchards or vegetable crops (Walter, Seaton and Mathewson 1938). Losses due to *Atta cephalotes* and *Acromyrmex octospinosus* in Trinidad citrus groves were considered by Cherrett (1968c) to amount to over \$600,000 (Trinidad dollars) per year in the 1960's or over 12 per cent of the annual crop value. The reduced carrying capacity of pastures in one state of Brazil caused by the grass-cutting and nesting of *Atta capiguara*, has been recently estimated by Amante (1967b) to be equivalent to 800,000 head of cattle. To put it another way, ten adult colonies take the food of one cow. Amante has estimated other damages by *Atta* species in Brazil. Cramer (1967), using Peruvian data, has concluded that leaf-cutting ant damage is comparable to that of migratory locusts.

Anyone who has tried to garden at almost any location in the American tropics has probably encountered leaf-cutter ants. The ants will cut most varieties of flowers and often will remove entire plants such as roses and zinnias. There are some plants that the ants will not ordinarily touch, such as beans, tomatoes, melons, and cucumbers. In some areas one cannot have a flower or vegetable garden without taking some measures to control the leaf-cutter ants, but it is impossible to put an accurate monetary value on such damage.

#### ADAPTATION TO URBANIZATION

While attines are most abundant in fields and forests, these ants have adapted well to the cities. The attractive plazas and city parks in Central and South America have preserved enough natural vegetation and nesting sites to enable many of the common species to survive. Spo-



FIG. 1. A large nest of *Atta sexdens* at the base of a tree in the Plaza de Lesseps, Panama City, in 1938. There were 14 such nests in this attractive city square at that time. The ants were still a dominant animal life in the Plaza in 1954 but in 1955 a major building program extinguished much of their foraging area and their numbers greatly dwindled in the 1960's. By 1971 *Atta colombica tonsipes* replaced *sexdens* here although *sexdens* still occurred in the city.

radic attempts at exterminating the large species may be successful, but the ants frequently invade from adjacent areas. Small and inconspicuous species often inhabit the patios of houses and any neglected or weedy lot is a potential haven.

The large nests of *Atta sexdens* in a central plaza in Panama City were so impressive in 1938 that I photographed them (fig. 1). The ants were dominant animals and foraged for leaves on the shade trees and also picked up starchy food dropped by humans. Everyone recognized them as an ordinary fact of life, and there seemed to be mutual tolerance between man and ant. In later years I noticed them gradually dwindling in numbers because of a growing building program that meant less and less space and vegetation for them. In 1966 they were confined to one or few colonies surviving behind masonry cracks and on the edges of a grassy recreational field. It is my belief that they were on this site long before the city was created and have shown an ability to survive for centuries in gradually diminishing space. They are still abundant enough in the suburbs.

The leaf-cutting *Acromyrmex* are the most common urban attines from Tucson, Arizona, south to Buenos Aires and Bahia Blanca, Argentina. The nests of *Atta* are so much more conspicuous than those of *Acromyrmex* that the importance of the latter is generally minimized

(Weber, 1967b). Wherever it can excavate an irregular cavity in the soil it can form its fungus gardens. Common nests are behind cracks in masonry walls where the ants are quite inaccessible for observations or control. Potted plants afford at least temporary nesting sites, and tiles covering the soil form excellent roofs for chambers and tunnels in the underlying moist soil. A young colony may go unobserved for two or three months because the ants are slow-moving, inconspicuously colored, and often collect plant material at night. These ants cause many tender garden plants to disappear overnight and they attack the spiniest shrubs as well. In six months a new colony started by a single fertilized female may grow to thousands of workers. Gardeners can control them if necessary, but extermination is difficult unless regular measures are taken for several years. The complete extermination of the ants would be regrettable since they are an animal feature of the plazas like the pigeons, and many people relaxing on the benches find their leaf-cutting and trails of interest.

In Trinidad, *Acromyrmex octospinosus* is clearly associated with cultivated land, whereas *Atta cephalotes* is primarily a forest ant. In one area of forest there were five nests of *Atta* and none of *Acromyrmex*; and in an adjacent, equal area of cultivated land, there were three nests of *Atta* and twenty-seven of *Acromyrmex* (Cherrett, 1968c). Only one species of each genus occurs in Trinidad, and the *Acromyrmex* is more difficult to control because its nests are smaller, more inconspicuous, and more numerous than those of *Atta*. A colony known to me on the campus of the University of the West Indies lived in the same inconspicuous site 1964 through 1970. My laboratory colonies of *Acromyrmex octospinosus* may produce new queens early in the second year which is one or two years earlier than the formation of new colonies by *Atta*.

Studies on the effects of *Atta* on pre-Colombian human ecology (e.g., Fautereau, 1952; Weber, 1969b) might well be extended to *Acromyrmex* although the early relationships of man and *Acromyrmex* would be much more difficult to trace.

Zoological gardens from time to time have displays of *Atta* or *Acromyrmex* colonies that are used to demonstrate the leaf-cutting habit. The New York Zoological Society had a successful exhibit in its Bronx Zoo and the present *Atta* colony in the Frankfurt, Germany, Zoo has been



thriving for some years. Marsh's Zoo in Panama in the 1930's had an inadvertent demonstration from local *Atta* colonies that thrived on the periphery in a natural state and invaded the cages for food given to the captive animals. In the 1960's the Buenos Aires Zoo in Argentina had *Acromyrmex lundii* in the wild state and they thrived in the Plaza Italia outside the main entrance.

#### LAWS RELATING TO LEAF-CUTTING ANTS

Several Latin American countries have passed laws designating certain species of leaf-cutting ants as "plagues," and the governments usually attempt extermination of the ants at the expense of the person owning or occupying the land, if he does not do so himself. Mexico many years ago produced a large color poster showing *Atta* at work and a good way to force poison gas into the nest with a stirrup pump. This was posted in all parts of the country and was an effective type of popular education.

Argentina passed Law 4863 of 27 July, 1909, designating "hormigas coloradas" (*Atta sexdens*) and "hormigas negras" (*Acromyrmex lundii*) as plagues.

Santa Fe Province, Argentina (1956), brought together its decrees of the past regarding the declared plagues. Decree 31.795 of November 4, 1907, dealt with "hormigas coloradas" and "hormigas negras," both being in this case *Acromyrmex* species. Law 4390 added *Atta vollenweideri* to the list of plague species. Bonetto (1959) considered the latter the most destructive in Santa Fe, and *Acromyrmex lundii* is clearly the most harmful in the Province of Buenos Aires.

#### METHODS FOR CONTROL OF LEAF-CUTTER ANTS

The earliest attempts at controlling leaf-cutter ants in the sixteenth century involved digging, burning, smoking, or flooding out the colonies; and these techniques are still used when no poison is available. White (1879) reported that the ants could be prevented from attacking a plantation by scattering exhausted substrate refuse from a different colony across the trails of the colony attacking the plantation. This technique will provide some temporary disruption but will not protect the plantation for many weeks as he claimed. Stahel and Geijskes (1939) suggested another method of ecological control

by forcing conidial spores from abnormal fungus gardens into nests, but there is no evidence that this will kill the garden or ants. No biological control has been thoroughly investigated, but on the basis of field and laboratory colonies, it appears that mites, Collembola, or phorid flies may be helpful in decreasing attine populations.

Early methods of chemical control were based mostly on the use of carbon bisulfide or burning sulfur, and, later, hydrogen cyanide and methyl bromide were recommended as fumigants. For treatment to be successful, all such chemicals must penetrate throughout the entire nest. This is virtually impossible because large nests frequently extend at least two meters deep and contain large dead air spaces. The chambers with gardens usually have entrances only at the bottom and it is not easy to displace the air in them.

The most successful method for killing leaf-cutting ant colonies entails the use of a slow-acting poison combined with soybean oil on an inert carrier such as ground-up corncobs, citrus pulp, bran, or flour. The soybean oil serves as an attractant, and the ants carry the particles into their nests where the poison, ingested by foraging and non-foraging ants, kills the ants over a period of weeks. The chemical currently used is dodecachlorooctahydro-1, 3, 4-methenol-1h-cyclobuta (cd) pentalene. Additional information about its use in controlling attines can be found in the papers by Amante (1966, 1967), Echols (1965, 1966) and Cherrett (1969). Indiscriminate or unnecessarily widespread use of this powerful chemical is greatly to be deplored because of the significant role of these ants in tropical ecology (Weber, 1966a, b). Ferguson (1970) refers to dangers in its use.

A type of biological control is reported to be employed in northwestern Mexico (Gentry, pers. commun.). The ants here are called *mochomas* and are presumably *Atta mexicana*. A local herb, originating in the state of Puebla, is called the "yerba del Pero" as it is used for poisoning dogs as well as ants. It has been identified by Gentry as *Senecio ehrenbergianus* Klatt. The herb is mixed in a bait and scattered about the entrances to the ant nests where the ants carry it down to their chambers. Whole nests are reputed to be destroyed by this treatment. Undoubtedly there are similar methods in other countries that have not appeared in the general literature.

EFFECTS OF GARDENING ANTS ON SOILS  
AND NUTRIENT CYCLE

From the standpoint of man, the gardening ants have two main beneficial aspects that somewhat compensate for their obvious depredations. First, they have direct beneficial effects on the soil, and second, the ants help cycle nutrients from vegetation back into the soil where they can be used again by plants.

The geologist Branner (1911) reported that *Atta sexdens* may have mounds containing as much as 117 cubic meters of earth. In the southern part of the State of Bahia and into Minas Gerais, Brazil, some mounds of *Atta* touched each other. In southern Brazil he found 53 mounds that occupied 2,064 square meters and included 2,225 cubic meters of soil. If this soil were evenly distributed, it would cover a hectare to a depth of 22 cm. *Atta sexdens* was so abundant on clayey soils and scarce or absent on sandy soils that the mounds could be used as indicators of the soil type and underlying parent materials. Amante (1967) and Bucher and Zuccardi (1967) have fully verified the quantities of soil mined by *Atta* (fig. 2).

While this is an unusually dramatic instance of overturning of soil, the principle applies universally to *Atta* throughout its range from Texas and Louisiana to Argentina. The smaller but more numerous mounds of other attines must also contain significant amounts of soil. Much soil must be washed from the mounds by rains so that the actual volumes excavated are much larger than the mounds.

It is difficult to assess the ecological effect of



FIG. 2. Mound of *Atta vollenweideri* on the pampas of Uruguay after a photo by C. S. Carbone. The ants harvest the leaves of trees and bushes as well as cultivated plants. Ant trails show on the left.

such mounds in any habitat. However, ants are one of the few animals that transfer soil mineral nutrients essential for plant growth to the upper layers where the nutrients can be utilized (Weber, 1966b). By their tunneling the ants also aerate the soil and create passageways for drainage or water penetration. The local animal agent chiefly responsible for taking organic matter down into the soil in tropical forests is probably *Atta*. Moreover, attines accelerate this process by which such plant material is broken down to allow re-use of the chemicals it contains. The extremely dense mats of fine roots growing in the refuse deposits outside nests of *Atta* attest to the abundance of nutrients in discarded substrate from the gardens.

COLLOQUIAL NAMES FOR LEAF-  
CUTTING ANTS

The importance and conspicuousness of leaf-cutting ants in Latin America are attested by the abundance of common names used in the different countries. The common English names are leaf-cutter ants, fungus-growing ants, and parasol ants (German: Blattschneider-Ameisen; French: fourmi fongueuse, fourmi champignonnistes).

The American terms are:

- Argentina—hormiga isaú, hormiga minera, hormiga podadora (*Atta vollenweideri*)
- hormiga negra (*Acromyrmex lundii*, *A. lobicornis*, and *A. hispidus*)
- hormiga colorado or reventona (*Acromyrmex striatus* and *A. heyeri*)
- hormiga overa (*A. lobicornis*)
- hormiga renegrida (*Acromyrmex ambiguus*)
- hormiga podadoras (*Atta* spp. or *Acromyrmex* spp.)
- Bolivia—chaka colorado (*Acromyrmex silvestri*)
- chaka negra (*Acromyrmex lobicornis*)
- Brazil—saúva mata-pasto (*Atta bisphaerica*)
- saúva preta (*Atta robusta*)
- saúva de mata (*Atta cephalotes*)
- saúva dos pastos (*Atta capiguara*)
- saúva or saúba (*Atta sexdens*)
- formiga mineira and carregadeira (*Atta* spp.)
- quenquen or quemquem (*Acromyrmex* spp. in general)
- formiga mineira, caiapo, formiga de raspa, formiga de monte (*Acromyrmex* spp.)
- quem-quem de arvore (*Acromyrmex coronatus*)
- British Honduras—wee wee (*Atta cephalotes*)
- Colombia—hormiga arriera, hormiga podadora (*Atta* spp.)
- Costa Rica—zompopos (*Atta cephalotes*, etc.)
- Cuba—bibijagua (*Atta insularis*)
- El Salvador—zampopos or zompopos (*Atta cephalotes*)
- Guatemala—zampopos or zompopos (*Atta cephalotes*)



- Guyana-cushi, cushi or acushi (*Atta cephalotes*, *A. sexdens*, *A. laevigata*)  
 Kuyammaru (Arawak Indian for *Atta* and *Acromyrmex octospinosus* or *A. hystrix*)  
 Honduras-wee-wee, zampopos or zompopos (*Atta cephalotes*)  
 Mexico-cuatlatla (in Morelos) (*Atta* spp.)  
 chancarra (in Guanajuato) (*Atta* spp.)  
 chicantana (in Oaxaca) (*Atta* spp.)  
 mochoma (in Chiapas) (*Atta* spp.)  
 sonteta (*Atta* spp.)  
 hormiga arriera (*Atta mexicana* and *A. cephalotes*)  
 Nicaragua-wee-wee (*Atta cephalotes*)  
 Panama-hormiga arriera or bachaca (*Atta cephalotes*, *A. colombica tonsipes*, and *A. sexdens*)  
 Paraguay-hormiga minera, isaú (*Atta vollenweideri*)  
 Peru-coqui (*Atta cephalotes* and *A. sexdens*)  
 Surinam-parasolmieren (Dutch for parasol ant) (*Atta cephalotes* and *A. sexdens*)  
 Trinidad-bachac (*Atta cephalotes*)  
 the small bachac (*Acromyrmex octospinosus*)  
 United States-Texas leaf-cutter ant, leaf-cutting ants, fungus-growing ants, parasol ants, town ants (*Atta texana*)  
 Uruguay-hormiga negra (*Acromyrmex lundii*)  
 hormiga de rodeo (*Acromyrmex striatus*)  
 hormiga colorado (*Acromyrmex striatus*)  
 Venezuela-bachaco (*Atta cephalotes* and *A. sexdens*)  
 pequenos bachacos (*Acromyrmex octospinosus*, *A. hystrix*)

#### TERMITE AND ATTINE ANT GARDENS COMPARED

Grassé and Noirot (1957) and Sands (1960) have given accounts of gardens of the termites, *Macrotermes mülleri*, *Protermes prorepens*, *Acanthotermes acanthothorax*, and *Ancistrotermes guineensis* in Africa. Exceptional color photographs of Grassé and Noirot show that the gardens are remarkably like *Atta* gardens in having the superficial and younger parts dark and the lower and senile parts paler. The most vigorous fungus growth may be in cells below the most recent additions to the garden or at the upper side of the comb ("meule").

Termite gardens, however, consist entirely of vegetal or vegetal-soil material that has passed through the digestive tract of the termites and is therefore fecal. Ant gardens consist of vegetal or insect fecal material to which the ant saliva and liquid fecal droplets have been added. The end product in both termites and ant gardens thus has fecal material as a significant biochemical contribution to the metabolism of the fungus. It is these nutrients that enable the fungus to compete with alien fungi. A similar metabolic need in the termite fungus is suggested by the studies of Grassé and Noirot and of Sands. The latter has also performed the type of

experiment performed with many attines (Weber, 1945, etc.) of giving the insects, deprived of their normal fungus, fungus garden fragments of another species. Gardens of *Ancistrotermes guineensis* that were sterile and lacked the fungus were clearly undernourishing the termites and they were then given parts of the garden with fungus of *A. crucifer*. Both garden and fungus were eaten but the fungus did not grow and was all consumed. It was not until the *guineensis* termites were given fragments of garden with fungus of another colony of their own species that the fungus (*Termitomyces*) appeared in their later fecal pellets and grew normally on the formerly sterile garden. As Grassé and Noirot had shown, the termite garden comb is a part of the food cycle and is re-eaten by the termites, the woody material becoming more assimilable by the fungus.

Earlier evidence by Grassé and Noirot (1955) and others led Sands to suggest that there are different degrees of symbiosis between termites and *Termitomyces*. The most intimate case is that of termites with hard, brittle gardens consisting of termite feces; in simpler cases the garden may be more clearly of woody fibers from chewed wood. In all cases, the inoculum of the fungus comes from spores brought in by foraging termite workers on their bodies. The new generation of fungus in ants originates from a mass taken by virgin females on their nuptial flight and spores are never involved.

Heim (1952) cultured the termite fungi, *Termitomyces striatus* and *schimperi*, and showed results that were somewhat similar to cultures of ant fungi from several of the smaller ant genera.

That success of the fungus-growing termites in developing large colonies is comparable to that of ants is indicated by the estimation that the maximum size of the African giant termite mounds (*Bellicositermes*) may be up to 1,200 cubic meters (Grassé and Noirot, 1949).

#### OTHER INSECT-FUNGUS RELATIONS

It might be expected that among the hundreds of thousands of insects other than ants and termites there might be other examples of symbiotic relationships to fungi. Among the best known are beetles and wasps that are associated with wood. This has led to studies because of their economic importance when they infest commercial stands of trees. Those that are regularly associated with fungi have been

reviewed by Francke-Grosmann (in Henry, 1967). They are:

1. The wood wasps, Siricidae and Xiphydriidae. The female wasps attack trees and lay their eggs some centimeters below the surface. The ovipositor has a sack at the base containing fungal spores which are then inserted with the egg in the tree. Larvae also may have fungus sacks or mycetangia containing fungal spores. The wood decays through the activity of the fungus.

2. Ship timber worms (Lymexylidae). These beetles infest timbers, the adults living free but the larvae boring into the wood. The female transmits the fungus when it lays eggs and the resulting larvae and the fungi weaken the wood.

3. Bark-feeding beetles (some Scolytidae). These feed on phloem and are associated with yeasts and blue-stain fungi. Some of the fungi may be free-living but others are transmitted as slimy spores adhering to the beetle's integument or passing undigested out of the gut. The female of *Ips* has a sack at the base of the mandibles containing fungal spores; in *Dendroctonus* there is a sack at the anterior margin of the prothorax containing spores. The beetle-fungus attack may kill infested trees.

4. Ambrosia beetles (some Scolytidae). Species of Xyloterini, Cortbylini, Xyleborini, and Web-bini in the Ipinae and species of tropical Scolyto-platypodinae tunnel into trees and lay eggs. The resulting larvae form their own burrows. These beetles live in an obligatory symbiosis with their special domesticated Ambrosia fungus. The main benefit is to the beetle since the fungus may also be free living. The fungus provides a rich and easily available food containing all important vitamins. The beetles have special sacks or pockets (mycetangia) in the body or even at the base of the legs that regularly contain the fungus. These may contain secretions that prevent the desiccation of the fungus. Ambrosia beetles have a number of guests or inquilines that take advantage of their burrows.

Ambrosia fungi from the beetles have been described by Batra (1967). Most are dimorphic, having a yeast and a mycelial phase. They resemble the fungus of the attine, *Cyphomyrmex rimosus*, in this respect (see chapter 8).

#### OBSERVATION NESTS

Field observations, indispensable as they are, need to be supplemented by observations and

experiments in the laboratory. It is always possible to pick up a few ants and a bit of their fungus garden, place them in some kind of glass container, preferably the flat Petri dish type (fig. 146), and bring them inside for later study. The material may be examined on the stage of a binocular stereoscopic microscope, preferably at comparatively low magnifications, such as 10 $\times$  to 40 $\times$ , and much may be learned.

A container must be used for study long enough to produce an environment suitable for the survival of both the ants and their fungus. The ants themselves may survive in a fairly dry atmosphere, provided they have access to drinking water, but the fungus garden needs a constant highly humid atmosphere. This may be obtained in a closed container that holds clean, white, and moist sand. The environment for the substrate and excavated soil or old substrate also has to be considered and in general a rather dry atmosphere (a relative humidity of some 20–50 per cent) is better for these parts of the nest; otherwise mold will soon form.

The well-known Janet and Fielde observation nests, long ago described, are suitable, if the above requirements may be met. Plaster of Paris nests may be better in some climates and were figured by Gallardo (1915) in Argentina. They may be constructed as a series of chambers with connecting tunnels and set vertically between panes of glass that can provide a humidity gradient. In 1934–1935 I used modified Janet-type nests in attine studies, consisting of simple wood frames between panes of glass (fig. 133), as well as Petri dishes for small species. These were opened partially and placed in a larger, enclosed arena. Later a three-chambered clear plastic container (lucite or plexiglas) was devised (Weber, 1956) that could be placed on the stage of a microscope (fig. 134). The larger chamber was kept empty and dry and substrate was periodically added to it through a side hole, usually kept closed with a rubber stopper. Many of the species have no difficulty in gnawing through ordinary corks. One of the other two chambers was also kept dry and with clean sand. The third was used for the garden and partly filled with clean white quartz sand kept moist. The ants excavated it as space was needed. Each chamber had a small hole connecting it with the one opposite.

Larger plastic containers were used for larger colonies and for a year or two converted laboratory mouse nests were used (fig. 136). These



were of clear plastic, 1,600 ml. in capacity, and were placed upside down on a plaster of Paris base. They were connected with one another by plastic tubes 2.5 cm. (one inch) in internal diameter. A colony could thus be accommodated as it grew. In recent years rectangular plastic boxes were used that were  $2\frac{1}{4}$  liters in capacity (figs. 137-138). These were bored for the same 2.5 cm. connecting tubes and two holes on the cover to take No. 5 rubber stoppers. In course of time even this tough rubber was chewed through by the ants. A dozen of these boxes may be used by one vigorous *Atta* colony of three years age (fig. 131). Soil or sand are unnecessary for most large colonies with established gardens.

#### MOVING THE ATTINE COLONIES

It was necessary one year to move the entire collection of living colonies from Pennsylvania to Wisconsin. The fungus gardens were in various containers at that time, but in any case they could not be tilted or jarred without serious damage. The nests were loaded in a station wagon, well insulated between layers of bedding

and winter clothes for a family of five. The two-day trip was made in hot weather and the colonies arrived in perfect condition.

On recent yearly trips to the tropics for new colonies there were similar problems of transport. The highly fragile garden should be placed directly into the container that will be used in transport. It must always be kept upright, since otherwise it will shift and be broken into pieces. Young colonies with queen are most successfully brought in. It is always a problem to keep the package from being jostled but I have had as many as four students traveling with me, each with a load, and have had much success with many species.

The colonies have been maintained in the laboratory under permit from the U. S. Department of Agriculture. This is necessary because of the ever-present danger of accidentally introducing harmful animals or plants into the country. Any quantity of soil or a natural product is a risk. The permit requires that the colonies be maintained under control in the laboratory and, at the end of the experiments, all be destroyed.

## 2. BODY STRUCTURE AND FUNCTION

### CASTES

The fungus-growing ants possess three distinct castes: workers, females, and males (fig. 3, 12). The largest workers of *Atta* often are called "soldiers" and they appear to function primarily for colony defense. However, the workers of *Acromyrmex* and *Atta* are polymorphic, range considerably in size, and show a gradual and continuous change from the smallest to the largest workers. As the workers become larger, their heads usually become disproportionately enlarged. Since there are intermediates between any two types of workers, they cannot be separated except into arbitrary categories. The terms soldier, maxima, media and minima workers are used here to designate only approximate groups of workers. These size groups will be discussed more fully below in the section on polymorphism of workers (p. 14).

The workers are all genetic "females," but that term will be used here only for the reproductive caste or queen that lays all the eggs develop-

ing into ants in a normal colony. Some workers, perhaps most of them, lay eggs that are eaten or have eggs in their oviducts that are eventually resorbed. If a queen dies or is removed from a colony, workers may lay eggs developing into males. Workers cannot be fertilized, and there is no evidence that workers can lay eggs which develop into workers.

Explanations for the caste and worker ratios in Hymenoptera have been advanced by investigators such as Spencer (1894) and Flanders (1970).

The female caste includes virgin queens which are usually winged or alate when found in a colony and the functional queens which are wingless or dealate. Most colonies contain only a single functional queen. However, when a wingless female is found in a colony one can determine whether she is a functional queen by observing whether she lays eggs which develop into workers or by dissecting her to determine whether she has been inseminated.

The only apparent function of the male caste is to fertilize the females on the brief seasonal mating flight. Males are short-lived and, if present in a colony, they always have wings. The males do not participate in any of the work inside or outside of the colony.

### STRUCTURE OF THE ADULT ANTS

The generalized attine worker is a spiny, dull reddish brown ant with a heart-shaped head and long, spindly legs (fig. 4). The mandibles are triangular with fine teeth on the cutting edges (fig. 7). Details of the mouthparts are



FIG. 3. Castes of *Atta colombica tonsipes* (after M. M. Martin *et al.*) Panama. Winged female at right, winged male at left, queen below, workers on periphery. The smallest workers tend the brood and garden, those of medium sizes excavate soil and cut leaves and the largest sizes, culminating in the soldier, defend the colony.

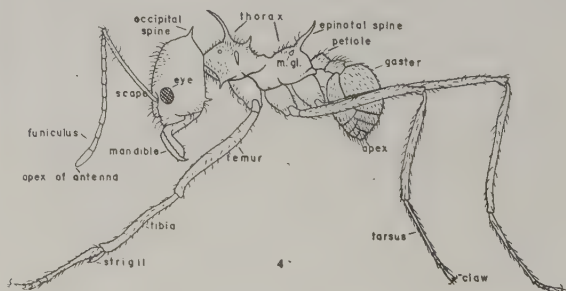


FIG. 4. An attine ant (*Atta cephalotes isthmicola*) with major parts labeled; m. gl. is the opening of the metapleural gland.

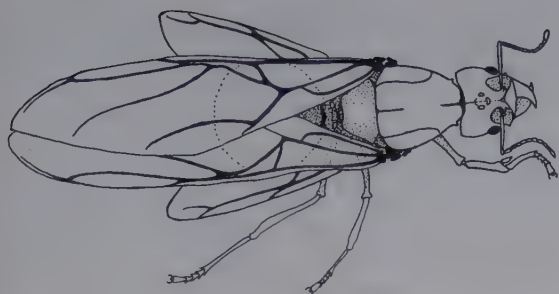


FIG. 5. Winged female of *Atta colombica tonsipes* from above. Length to wing tips 35 mm. Panama.

to be found in Gotwald (1969). The antennae are long and slender and are held forward with the tips waving about when the ant moves. The base of each antenna is concealed by a lobe of the frons (frontal lobe). The antennae of some species can be folded into antennal scrobes or grooves on the sides of the head. The compound eyes are small, convex, and situated near the middle of the head. The males and females have ocelli in addition to compound eyes. No ocelli occur in the worker caste except for a few examples in *Acromyrmex* and often in the *Atta* soldier. When a vestige occurs, it is most often the anterior one. In almost all specimens the anterior ocellus is double, indicating that ancestral insects had two pairs of ocelli of which the anterior later fused (Weber, 1947a). Characteristically each occipital corner

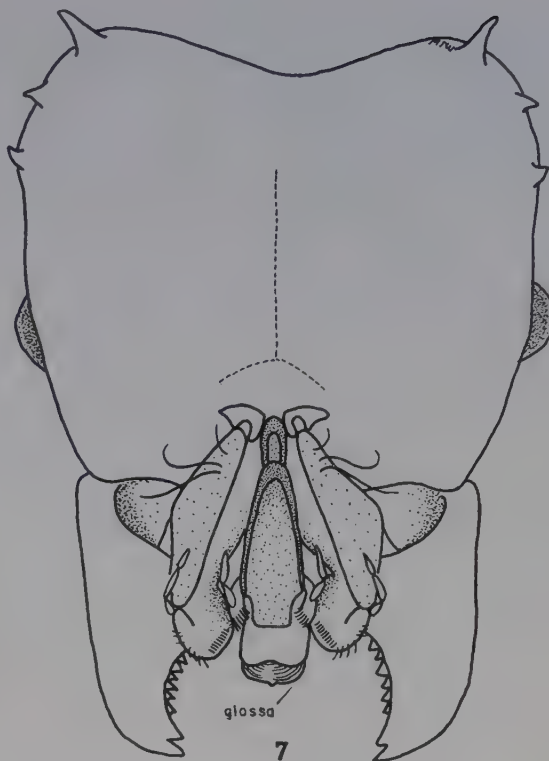


FIG. 7. Head of *Acromyrmex lundii* from behind showing mouthparts. The most central is the expanded glossa or tongue covered with a fine rasp. At the sides are accessory mouthparts, also with files and fine hairs that rasp the fungus when feeding. Only liquids pass into the body. Argentina.



FIG. 6. Head of male of *Trachymyrmex jamaicensis* showing large eyes and ocelli, feeble mandibles, and long antennae typical of male attines. The head is compressed behind from lack of large mandibular muscles. Bahama Islands. The male has 13-segmented antennae; two of the above on each side were actually double.

bears a spine or tubercle, and usually a smaller spine arises in front of each occiput or rear of head. A prominent pair of spines occurs at the rear of the thorax or mesosoma, the epinotal spines, and they may protect the small petiole and post-petiole. The upper or basal part of the epinotum frequently has a carina, sometimes tuberculate, on each side. Its form is often obscured by hairs or spines. The rear part of the abdomen or gaster is small and ovate with an inconspicuous sting.

The males and females or queens are only slightly larger than workers of the species, except in *Atta* which has greatly enlarged reproductives (figs. 3, 12). Compared with the workers, the females are more coarsely sculptured (fig. 8) and have larger compound eyes and three ocelli in the middle of the head (fig. 9). Epinotal spines are reduced. The gaster is more nearly spherical and proportionately larger to accommodate the larger ovaries. The wings extend



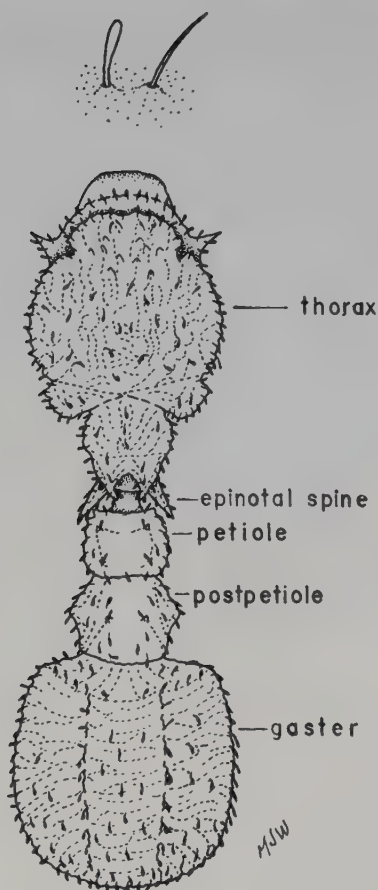


FIG. 8. Trunk of female of *Trachymyrmex zeteki* from above showing spines and hairs; two hairs are shown enlarged at top. Panama.

past the body and have usually brown membranes.

Males are consistently smaller than the females. They are black or dark brown in most cases or at least darker than the other castes. Mandibles are triangular but with reduced dentition, and more elongate than those of the females and workers. The eyes are much larger, but the heads of the males are smaller than those of the females or large workers (fig. 6). The ocelli form a protruding triangle on the frons. The thorax is proportionately smaller than that of the female but with reduced epinotal spines, sculpturing, and tubercles. Wings and legs are similar to those of the female. The genitalia are large and exserted.

The powerful adductor muscles of the mandibles fill most of the head of workers. Generally, the larger the head the more effective cutting

mandibles the ant possesses. The mandibles of *Apterostigma* workers are weak and used mostly for carrying particulate fragments of substrate, and the head is not heart-shaped.

The sting is small and inconspicuous, barely extending beyond the hairs at the apex of the abdomen in some cases but twice as stout as the hairs. It is capable of slight external movement. It is difficult to separate attempts to sting from attempts to deposit liquid excrement which seem in any case synchronous acts. The gaster is bent under and forward and executes repeated thrusting movements, when the sting is against another animal in the pose of a typical stinging ant. A film of moisture on the insect or other animal that is the victim shows that the venom sac has been discharged. My khaki trousers have been conspicuously dotted by deposits from the gut and contents of the venom sac of *Acromyrmex ambiguus*. The theory that the sting has been replaced by the mandibles as a major asset in defense was advanced by Hermann *et al.* (1970).

The wings are useful for generic determinations (Weber, 1966a). The fore wing posterior or distal to the stigma has usually two closed cells that have been referred to by Wheeler, Forel, and Emery as the cubital and radial. Students of the honey bee and other Hymenoptera refer to them as marginal cells No. 1 and 2, respectively. These two cells tend to have a characteristic



FIG. 9. The large female of *Atta cephalotes* L. held on the author's finger and with one of her attendant minima workers which refused to leave her. A female laying eggs weighed 346 milligrams alive and the minima workers weighed 0.4 mg. Trinidad.



shape in each genus and to be compact in the most primitive and elongate in the higher genera.

### *Integument*

The integument is generally dull and roughened by spines, tubercles, and sculpturing (fig. 8) but a few workers are smooth enough to shine. Most species are hairy, and *Apterostigma* and *Sericomyrmex* are silky in appearance from the abundant flexuous hairs. Several small genera have spatulate hairs appearing as appressed silvery scales on some species. In addition to the upright hairs there is commonly a fine pubescence.

Many Attini and especially *Trachymyrmex* exhibit a variable integumentary condition known as a "bloom." This appears as a whitish granular deposit or scattered minute white areas. It gives the ant a grayish, dusty appearance to the naked eye. Under the microscope, however, the integument is seen to be immaculate and ferruginous, with the areas of bloom occupying only a small part.

More concentrated bloom on the prosternites was seen in Trinidad in a colony of *Trachymyrmex ruthae*. The workers were a dark brown, and the silvery prosternites could be seen as the ants walked upside down on the glass ceiling of the observation nest. The contrast was striking and suggested a luminescence. Subsequently this condition of the prosternite has been seen in less striking form in many species. In *T. septentrionalis*, for example, it is of regular but variable occurrence. Young callow workers do not have it. Females exhibit the condition as workers do.

It is possible that this bloom is a crystalline wax as figured by Locke (1965) who has diagrammed the way in which it may move through the layers of the cuticle and be deposited on the outer surface.

### *Eyes, Antennae, and Stridulatory Apparatus*

The compound eyes of attines are only moderately developed compared with those of ants in general. Like those of other insects and vertebrates, the eyes of attines are precocious in development and are the first part of the body to become pigmented in the pupa. This feature can be used to determine the age of pupae (see Life Cycle, p. 39). When the eyes are first becoming pigmented, the individual ommatidia may be distinguished as dark spots under a

stereoscopic microscope. There were 168 in one eye of a female pupa of *Trachymyrmex septentrionalis*. Later these expand to form one apparent continuous dark mass. Each facet has a convex outer integumentary lens. Although the eyes appear to be adequately developed to see some images, the extent that attines use vision is unknown.

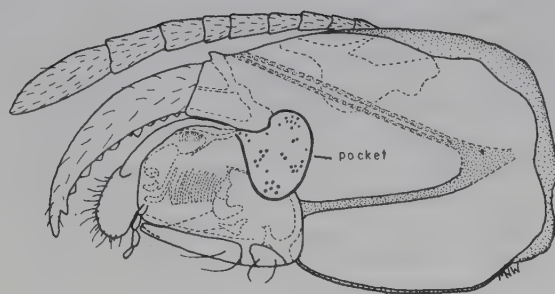
The terminal tips of the antennae appear to bear the sense organs used more than the mouthparts for detecting the suitability of substrate or fungal food. Since the apices are frequently combed by the strigil and then drawn across the moist mouthparts, they are normally clean and moist. This use of antennae, therefore, resembles the combination of the mammalian use of the tongue and nose for taste and smell.

As the ants walk about, the antennae are held outspread and are directed from side to side. Slow motion pictures show a whiplike action of the antennae and their occasional independent use. The apices are gently and carefully brought close to the object being perceived.

Attines apparently have a stridulatory organ consisting of a filelike structure on the dorsal surface of the first gastric segment and a scraper on the underside of the posterior margin of the postpetiole (fig. 8). When the gaster is moved up and down a faint stridulation or squeaking noise is produced. Haskins and Enzmann (1938) and Haskins (1939) published illustrations of the files of ants from a variety of genera.

The first thorough investigation of the stridulation of any species of ant is that by Markl (1965, 1966, 1967) for *Atta cephalotes*. No ant is apparently able to detect sounds transmitted through the air but can detect substrate vibrations. Markl reported that *Atta* workers were attracted to a vibrating glass rod and also to buried workers. The primary known function of the stridulation is as an alarm attracting other workers to dig up the buried ant making the noise.

We have used the ant stridulations as a class demonstration to students. The stridulation can be easily heard by picking up a worker by the head and holding it close to one's ear. Each of the six species of *Atta* or *Acromyrmex* we tested had a characteristic pattern distinguishable on oscillograms. The loudest was *Acromyrmex ostospinosus*, and *Atta cephalotes* produced the highest frequencies.



10

FIG. 10. Section of head of *Trachymyrmex septentrionalis* showing infrabuccal pocket emptying into mouth above the mouthparts. The pharyngeal tube leading to the thorax is not shown. The V-shaped structure is the internal skeleton.

#### *Infrabuccal Pocket*

The infrabuccal pocket, a blind evagination below the anterior part of the pharynx at the mouth opening, is characteristic of ants but of special importance in the fungus-growing ones (fig. 10). This pocket receives the detritus from the grooming operations of the ants (e.g., Bailey, 1920). It is a consistent and impressive finding that ants throughout the world and of all kinds are literally immaculate when carefully removed from the nest in nature. It does not matter whether the nest is buried in dry and dusty soil, in wet boggy humus or in rotted wood in tropical forest, the ants are always clean externally. The ants may have a smooth and shiny integument or one covered with hairs and spines.

Important as grooming and the infrabuccal pocket are to ants in general, this activity and the structure are used by the fungus-growers for removing pathogens that might inhibit or kill the ant fungus. The attine garden is always in a moist chamber and, being of an organic nature, presents an ideal environment for many organisms besides the ant fungus. Other fungi find it entirely suitable as food.

The infrabuccal pellet may be squeezed from the head of a freshly killed ant and the contents placed on a microscope slide. Commonly the pocket contains unrecognizable and finely divided debris, angular soil particles, and spores. Two pellets from *Atta sexdens* workers of a laboratory colony, under 430 X magnification, contained two types of fungal spores and cassava starch grains.

When workers of *Trachymyrmex septentrionalis*

were dusted with carborundum powder (commercial 13/F having a particle size range of 0.03–0.15 mm.), the ants immediately proceeded to clean themselves using the tarsal hairs and the strigils on the fore legs. These were drawn through the mouthparts to clean them and the powder collected in the infrabuccal pocket. Two worker ants dusted in the afternoon cleaned themselves appreciably within the next hour, and overnight they deposited ten pellets. The pellets were somewhat kidney-shaped, approximately 0.16–0.17 mm. by 0.25–0.27 mm., and consisted of the characteristic steely carborundum. The same type of experiment was tried with plaster of Paris and other dusts. The ants remained where they were and cleaned themselves before entering the garden chamber.

#### POLYMORPHISM OF WORKERS AND DIVISION OF LABOR

Workers of some of the attines are monomorphic in that there is little range in size within the

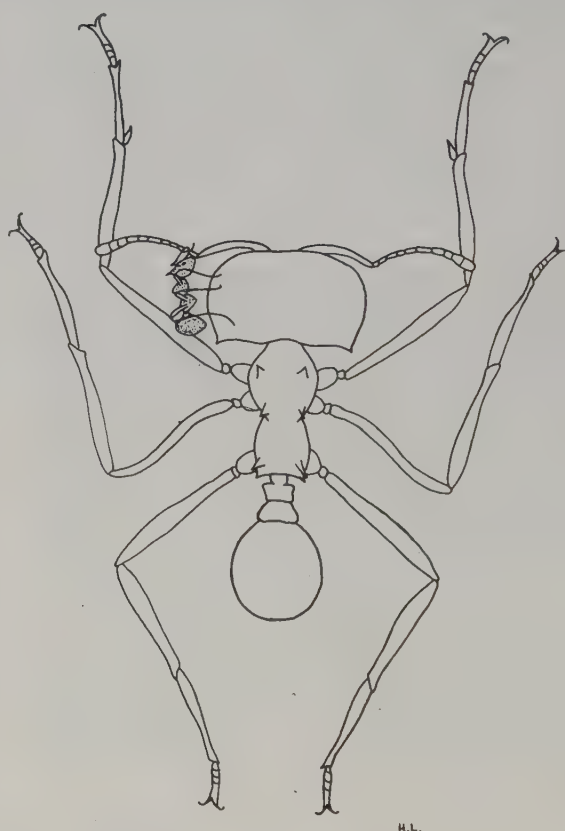


FIG. 11. Minima of *Atta cephalotes* riding on the head of a soldier. The minima commonly sponge the integument of the soldiers as they do the queen.



workers of a colony, and the largest and smallest workers are similar in shape. *Atta* and *Acromyrmex* exhibit the maximum amount of polymorphism within the tribe (figs. 11, 12) (e.g., Wilson, 1953). There is a rough correlation between the size of the workers and the tasks performed within and outside the nest. This type of correlation is usually called division of labor and is considered an advanced form of social organization that is probably evolving in the direction of increased specialization leading eventually to distinct morphological castes with specific duties.

The smallest workers of *Atta* and *Acromyrmex* are about 2 mm. long when an ant in a natural walking position is measured. Arbitrary size classes, to the nearest millimeter, which I have



FIG. 13. Soldier of *Atta cephalotes* showing the tufts of golden hairs on each side of the front of the head and the powerful mandibles capable of cutting shoe leather. From the author's laboratory table. (Phot. C. W. Rettenmeyer.)

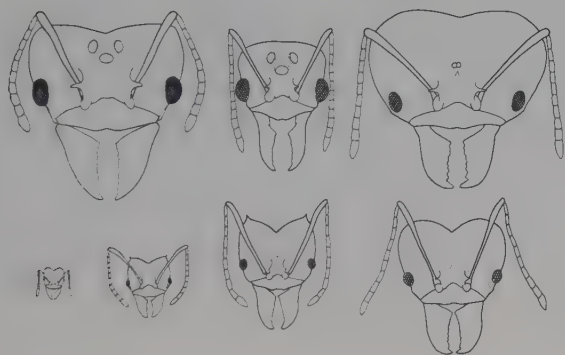


FIG. 12. Front view of heads of castes of *Atta cephalotes*, to scale. Top row, left to right, female, male, soldier (note median paired simple eye or ocellus). Bottom row, left to right, minima, two media, and maxima workers. Trinidad.

used for *Atta* are: minima, 2–3 mm.; media, 4–6 mm.; maxima, 7–9 mm.; and soldier, 10–15 mm. (fig. 13). *Acromyrmex* are somewhat smaller, with the maxima workers 7–10 mm. long (fig. 14).

Weights of a number of live attines in vials have been ascertained with a semi-micro balance. The smallest monomorphic species weighed to date is *Cyphomyrmex costatus* with an average of 0.11 mg. each for ten workers. Three males of this species averaged 0.24 mg., and three alate females averaged 0.47 m. Ten workers of *Sericomyrmex urichi* averaged 1.97 mg. with the largest worker weighing 2.62 mg., a male 2.85 mg., and a winged female 7.62 mg. Ten workers of *Trachymyrmex septentrionalis* ranged from 1.01–2.41 mg. with an average of 1.61 mg.



FIG. 14. Worker of *Acromyrmex octospinosus* attempting to bite the author's finger tip. The ant has engaged the claws of all six legs as well as the mandibles in the skin. (Phot. C. W. Rettenmeyer.)

Soldiers of *Atta cephalotes* weighed 38.39–92.00 mg., those of *isthmicola* 67–103 mg., and those of *sexdens* 22.48–63.90 mg. An ovipositing female of *A. cephalotes* weighed 346.34 mg. or about 825 times the weight of her smallest adult offspring; three of *sexdens* weighed 262, 271 and 289 mg.; *colombica* were 147–194 mg.

In all polymorphic species of attines, there is an inverse correlation between the length of the worker and their numbers in the colony. Soldiers are the least abundant but are so conspicuous that they appear to be a larger proportion of the colony. Whenever a colony of *Atta* is disturbed, the soldiers are usually attracted to the site of the disturbance. These large ants will run out of the nest entrances and attack anyone attempting to dig up the colony. The smallest ants never leave the nest, often immobilize or “freeze” when the nest is disturbed, and are very difficult to see among the garden and soil particles.

The soldiers very rarely cut or carry leaves or other objects. They sometimes go out on trails or cluster around nest entrances, but their primary function is to guard the colony against predators or objects disturbing the colony. They may “attack” and help remove an object like a fallen leaf or twig that blocks an entrance or trail.

The media workers do all the cutting and transporting of leaves and other large pieces of substrate as well as the removal of old substrate or dead ants from the nest. This group excavates the nest, helps construct the garden, and also defends the colony.

The minima workers are the most versatile group in an *Atta* colony. They will carry small fragments of substrate and dead minima workers, and are the most important group in caring for the brood and fungus garden. J. and M. Martin have shown (1970a and b) that minima workers of *Atta colombica tonsipes* have enlarged recta and deposit relatively large fecal droplets on the fungus garden.

Most of the minima workers stay within the nest, but some accompany the larger workers on

the trails. These minima workers do not carry leaves but will often ride back to the nest on leaves carried by larger workers. Although it has usually been assumed that these workers are simply “hitching a ride” or “joy-riding” and detrimental to the efficiency of the foraging, these riding ants appear to serve at least two functions. While the minima workers are riding they are also licking the surfaces of the leaf fragment. This may be adding enzymes favoring the growth of the fungus and certainly must clean off debris and alien organisms. This function was first implied by Stahel and Geijskes (1939) and Stahel (1943), and has been supported by my own and my students’ observations. While licking the leaf, the workers probably are ingesting small amounts of food from the plant material. The licking continues when the leaf is finally deposited within the nest. In addition, perhaps it is advantageous for the minima workers to ride in with the leaves since it insures that more of these workers are present to work on the fresh material.

A column of *Atta cephalotes* that was carrying rose leaf sections to a laboratory nest was watched for two continuous hours. During this time 95 of 99 leaf pieces seen being carried had minima workers riding on them. Most pieces had a single worker but one had 7, and there were 131 minima workers on the 95 leaf fragments. Many of these ants were clearly seen to be licking the fragments.

Another function of the riding minima workers is that they fend off the parasitic phorid flies that hover over the columns of ants and nest entrances (Eibl-Eibesfeldt, 1967). Some of these flies are known to lay eggs in adult ants in which they develop as internal parasites. Others live as adults and larvae in the nests of the ants, and it is not known whether they lay eggs on the ants or leaf pieces. The minima workers rear up on their middle and hind legs and fend off the flies with the front legs, antennae, and mandibles. The soldier and media workers show similar behavior when they are not carrying leaves.



### 3. CLASSIFICATION AND DISTRIBUTION

Taxonomists place all ants in one family, Formicidae, divided into about seven subfamilies including the Myrmicinae to which the fungus-growing ants belong. That subfamily is characterized by having two small segments, the petiole and postpetiole, between the thorax (mesosoma) and gaster (fig. 4). The fungus-growing ants are all in the tribe Attini which differs from most other myrmicines by having 11-segmented antennae in the worker and female. Most attines have a cordate or heart-shaped head with a spine at each occipital corner, possess spines on the thorax, and are a dull brown color.

The tribe Attini includes 12 genera, some 180 to 200 species, and at least 80 subspecies. Many of the subspecific names may be useful to indicate geographical races within a species while some subspecies may eventually be elevated to species or found to be invalid and dropped from the literature.

The Attini differ from all other ants by their growing of fungi, and the members of the tribe share a number of morphological features. They have not clearly been derived from any other ants, but the fungus-growers closely resemble the common myrmicine harvester ant, *Pheidole*.

Because of the difficulty in identifying single specimens of worker ants, one should always try to collect a series including the largest workers or soldiers and the males and females. The figures here<sup>1</sup> and in Weber (1966a) may assist in identifying many of the ants. Most attines can be readily identified to genus using the key in the appendix but in a large collection of miscellaneous specimens there may be a few that cannot easily be keyed.

As in other groups of plants and animals, this tribe of ants has undergone nomenclatural changes that accompanied more detailed study and increasing knowledge. The change with the most unfortunate consequences is alluded to in chapter 8, where the *Atta discigera* of Moeller (1893) has since been universally accepted by myrmecologists as belonging to *Acromyrmex*. The fungus of *Atta* in the modern sense may not be the same as Moeller's.

<sup>1</sup> Most of the figures used here have been drawn under my direction by students Suzanne Tubby and Marilyn Warkentin.

An older name for *Atta* was *Oecodoma*. *Atta* itself formerly was the comprehensive generic term for such present-day full genera as *Acromyrmex* and *Trachymyrmex*. The latter and three other genera were placed under *Cyphomyrmex* in Emery's important work of 1921.

Revisionary studies by Kempf and myself, listed in the bibliography, are of minor concern here except where general biological information and nest photographs are involved. Among these changes are:

*Mycetophylax brittoni* and subspecies are *M. conformis*

*Apterostigma angulatum* and *dubium* are *A. dentigerum*

*Apterostigma wasmanni* of Trinidad is *A. auriculatum*

*Sericomyrmex wheeleri* is *Trachymyrmex wheeleri*

*Trachymyrmex phippsi* is *Trachymyrmex diversus*

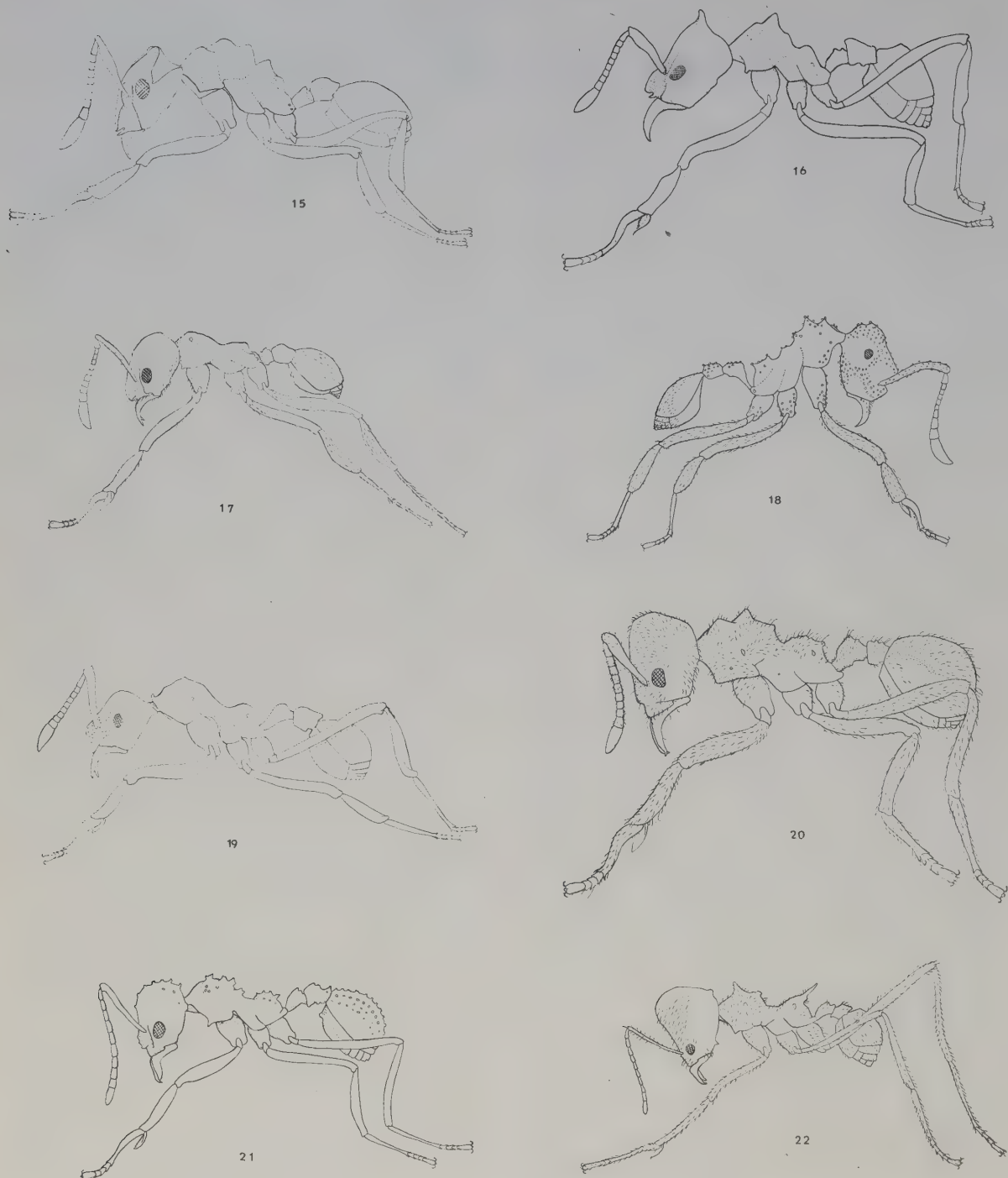
*Acromyrmex* (Moellerius) *balzani* and subspecies probably belong to the species *landolti*

*Atta cephalotes isthmicola* appears to be valid and *A. colombica tonsipes* may be treated as a valid name until type material of *colombica* is produced and proved to be the same.

#### GENERA OF ATTINES AND THEIR DISTRIBUTION

The sequence of genera should be one that reflects the origins and natural relationships. Since we have no fossil record, we are forced to rely on a combination of anatomy and ecological and behavioral evidence for relationships (Weber, 1958d). No arrangements can thus be deemed perfect to all people since each will place different values on the characteristics of the ants. The following sequence is used here: (1) *Cyphomyrmex*, (2) *Mycetosoritis*, (3) *Mycetophylax*, (4) *Mycocetopus*, (5) *Mycetarotes*, (6) *Myrmico-crypta*, (7) *Apterostigma*, (8) *Sericomyrmex*, (9) *Trachymyrmex*, (10) *Acromyrmex*, (11) *Pseudomyrmex*, and (12) *Atta*.

Following each genus the approximate number of species and a list of figures of adults and distribution maps are given.



- FIG. 15. Side view of *Cyphomyrmex rimosus transversus* worker. Venezuela.  
 FIG. 16. Side view of *Cyphomyrmex bigibbosus* worker. Guyana.  
 FIG. 17. Side view of *Mycetophylax conformis* worker. Trinidad.  
 FIG. 18. Side view of *Myrmicocrypta ednaella* worker. Panama.  
 FIG. 19. Side view of *Apterostigma calverti* worker. Panama.  
 FIG. 20. Side view of *Sericomyrmex urichi* worker. Trinidad.  
 FIG. 21. Side view of *Trachymyrmex cornetzi* worker. Trinidad.  
 FIG. 22. Side view of *Atta cephalotes opaca* soldier. Colombia.

- (1) *Cyphomyrmex* (30 species) (figs. 15, 16, 31, 44):

The genus *Cyphomyrmex* is large, heterogeneous, and widely distributed. One species, *C. rimosus* including its subspecies, is unique in culturing a fungus in the form of a yeast. It is also the most widely distributed attine, ranging from Florida and Texas to Argentina. In this genus the workers have unusually large and broadly separated frontal lobes and complete antennal scrobes. The thorax generally has rounded tubercles instead of spines.

- (2) *Mycetosoritis* (5 species) (figs. 45, 192):

The genus *Mycetosoritis* is represented by a species in Texas and others in Brazil. The genus appears to relate some *Cyphomyrmex* species with *Trachymyrmex*. It has been little studied.

- (3) *Mycetophylax* (7 species) (fig. 17, 32, 47):

The genus *Mycetophylax* lives primarily in the semi-desert or grasslands of interior South America as far south as the state of São Paulo, Brazil. One species, *M. conformis*, on Trinidad and other islands in the Caribbean is adapted for living in the sand just above high-tide level and uses grass for its gardens. The genus has not been found in Central America. The workers lack spines except for the epinotal pair.

- (4) *Myocepurus* (4 species) (figs. 45, 191):

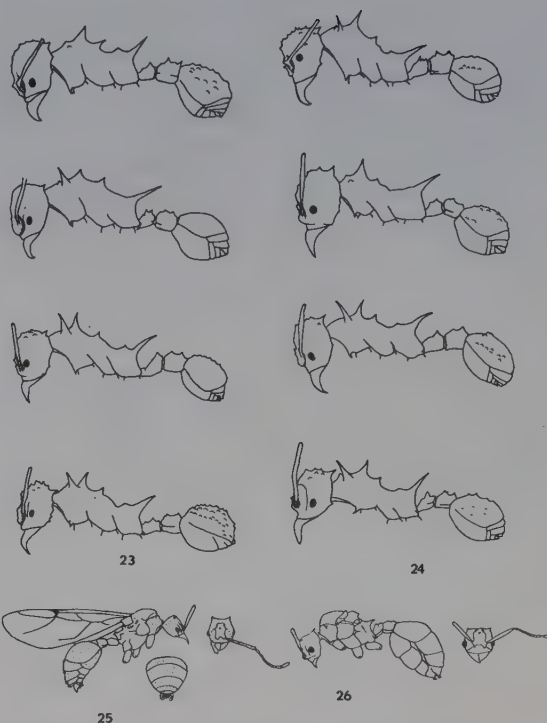
The genus *Myocepurus* is South American with the exception of *M. smithi*, found in the Caribbean and Panama. The ants are small-eyed and unusually spiny.

- (5) *Mycetarotes* (2 species) (figs. 45, 190):

The genus *Mycetarotes* contains two Brazilian species, one of which has been taken in north Argentina. The biology is little known, but the fungus gardens of this and the two preceding genera appear similar in major respects.

- (6) *Myrmicocrypta* (20 species) (figs. 18, 44):

The species of *Myrmicocrypta* are small, spindly ants with elongate heads that are rounded behind. The eyes are small and strongly convex. Spines or tubercles are conspicuous on the thorax and bear scalelike hairs which are characteristic of the genus. Males have huge hemispherical eyes, and the head is strongly sculptured behind. The ants seem to



FIGS. 23-24. Eight species of *Acromyrmex* from Argentina in side view to show differences in spines between the species (after Bonetto). 23: Top to bottom, *fracticornis*, *striatus*, *heyeri*, *hispidus*. 24: Top to bottom, *lobicornis*, *ambiguus*, *lundi*, *coronatus*.

FIGS. 25-26. *Pseudoatta argentina* male and female (after Gallardo). The ants are parasitic upon *Acromyrmex lundi*.

be largely of the forest, but the biology of only two species has been studied.

- (7) *Apterostigma* (27 species) (fig. 19, 33, 44):

The species of *Apterostigma* are the only completely nonspiny fungus-growers except for *A. epinotale* which has distinct but short epinotal spines. All species have small frontal lobes that conceal the antennal insertions and have heads evenly rounded at the occiput. Workers and females are hairy or pilose. The males have small heads with disproportionately long antennae and *Apterostigma* is characteristic of humid tropical areas.

- (8) *Sericomyrmex* (19 species) (figs 20, 34, 44):

Species of *Sericomyrmex* look like unusually smooth and silky *Trachymyrmex*. Their heads, however, lack occipital spines and are heart-shaped or cordate in outline. The pronotum is high and convex anteriorly and surmounted



by a pair of spines. The males have unusually small heads with almost hemispherical black eyes and the wings of both sexes are dark brown. The genus has recently been shown to exceed *Trachymyrmex* in colony population and size of fungus gardens and it is not primitive as formerly stated but is closely related to *Trachymyrmex*. *Sericomyrmex* is restricted to the continental tropics.

(9) *Trachymyrmex* (37 species) (figs. 21, 35, 36, 46):

The ants of the genus *Trachymyrmex* are generally spiny. The head always has a number of spines or sharp tubercles posteriorly. The thorax is spiny, in some species much as in *Acromyrmex*, and these spines often themselves bear tuberculate hairs. The gaster is more or

less densely tuberculate. The female is not greatly larger than the worker, being distinguished most conspicuously by her thicker thorax. The males are much smaller and darker. The ants resemble the comparable-sized *Acromyrmex* but the mandibles of the latter tend to be more massive and, moreover, the species of *Trachymyrmex* are monomorphic. From comparable sizes of *Atta* the ants are distinguished by the tuberculate head and gaster. There are more species of *Trachymyrmex* than in any other genus of attines, and they are distributed from the United States to Argentina.

(10) *Acromyrmex* (24 species) (figs. 23, 24, 37, 38, 39, 47):

The genus *Acromyrmex* is broad in distribution and comparable to *Atta* in importance, bio-

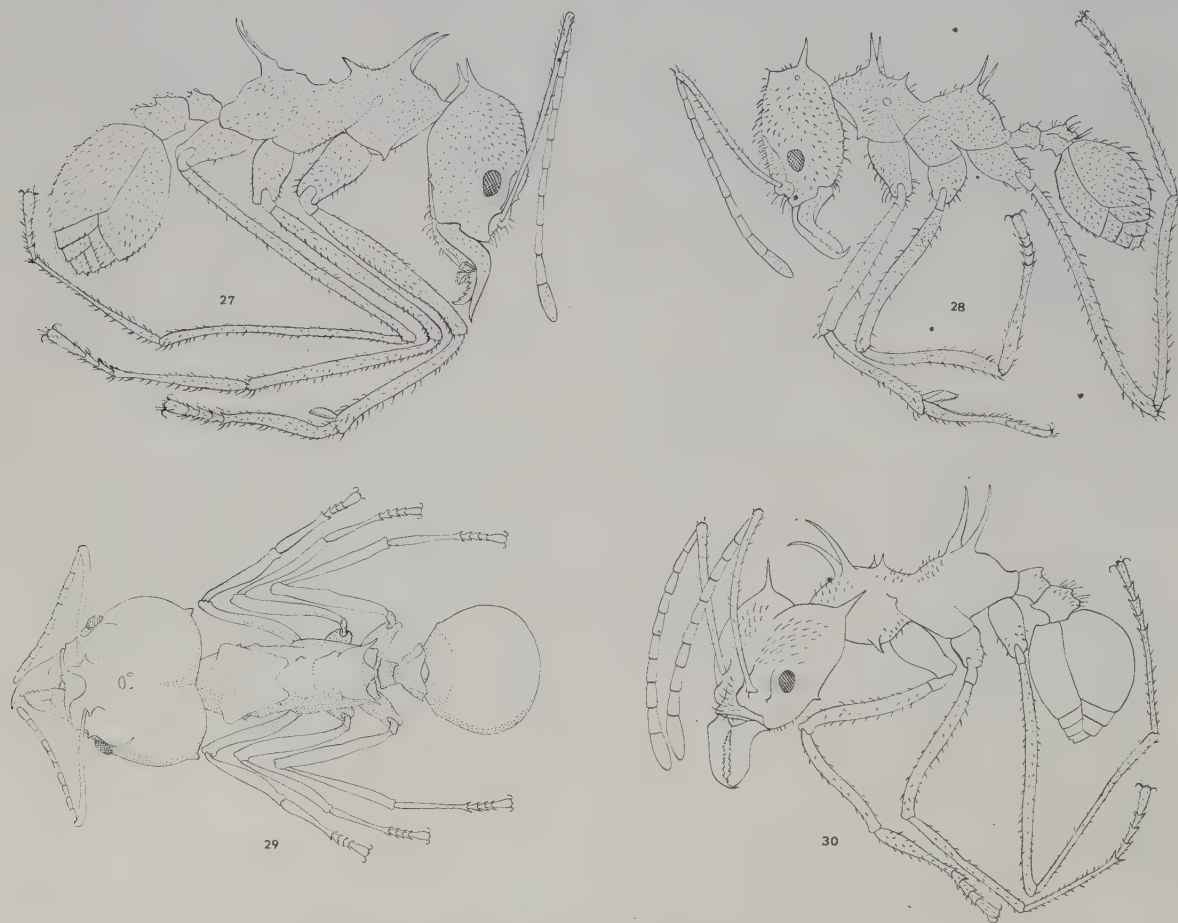


FIG. 27. Side view of *Atta colombica tonsipes* worker. Panama.

FIG. 28. Side view of *Atta sexdens* worker. Panama.

FIG. 29. View from above of *Atta cephalotes isthmicola* soldier. Panama.

FIG. 30. Side view of *Atta cephalotes isthmicola* worker. Panama.



- FIG. 31. The head of the *Cyphomyrmex bigibbosus* worker. Guyana.  
 FIG. 32. The head of the *Mycetophylax conformis* worker. Trinidad.  
 FIG. 33. The head of the *Apterostigma calverti* worker. Panama.  
 FIG. 34. The head of the *Sericomyrmex urichi* worker. Trinidad.  
 FIG. 35. The head of the *Trachymyrmex jamaicensis* worker. Bahama Islands.  
 FIG. 36. The head of the *Trachymyrmex jamaicensis* female. Bahama Islands.  
 FIG. 37. The head of the *Acromyrmex* (*Moellerius*) *landolti* worker. Venezuela.  
 FIG. 38. The head of the *Acromyrmex* (*A.*) *hispidus* worker. Argentina.  
 FIG. 39. The head of the *Acromyrmex* (*A.*) *lundi* female. Argentina.  
 FIG. 40. The head of a media worker of *Atta colombica tonsipes*. Panama.  
 FIG. 41. The head of the soldier of *Atta sexdens* from Guyana.  
 FIG. 42. The head of the worker of *Atta cephalotes opaca*. Colombia.

logically and economically. Emery (1905), Santschi (1925), and Gonçalves (1961) have published taxonomic studies on the South American species. The genus includes species in highly diverse habitats ranging from lowland rain forest and grassland to deserts and high Andean mountains. The typical subgenus, *Acromyrmex* of Central and South America, comprises most of the species, including the most important economic species, *A. lundi*, of southern South America, and *A. octospinosus*. The latter species ranges throughout most of South America and has been found on Trinidad, Tobago, Curaçao,

Guadeloupe, and Cuba. The other sub-genus *Moellerius* differs from *A. (Acromyrmex)* by having short, stout mandibles, not sinuous on their outer border, and by lack of lateral spines above the eyes of the worker. One species, *A. landolti*, of which *balzani* appears to be a synonym or a subspecies, ranges throughout central South America from Colombia to the south half of Brazil and Paraguay. The most common grassland and semidesert fungus-growing ants are in the two subgenera of *Acromyrmex*. Although the habitats appear ecologically similar, the species vary in the extent to which they collect

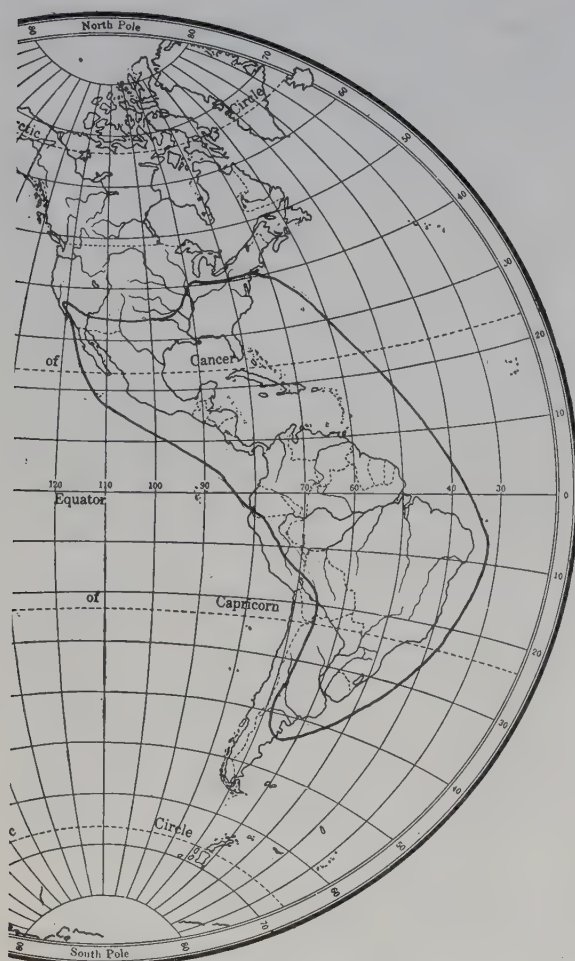


FIG. 43. The distribution of the Attini or fungus-growing ants in the New World.

grass; and some, such as *A. (Moellerius) versicolor* in arid parts of southwestern United States, collect pieces of leaves from bushes and herbs rather than from grasses.

Species of *Acromyrmex* are highly polymorphic in body size and in the size of their spines and tubercles. While they generally resemble some *Trachymyrmex*, the polymorphism of their workers and their much larger nests and gardens make separation easy. The females and males are also much larger than those of *Trachymyrmex*.

(11) *Pseudoatta* (1 species) (figs. 25, 26):

The only species, *Pseudoatta argentina* Gallardo (1916), was redescribed by Bruch (1928). It appears to be a social parasite on *Acromyrmex lundii* and is known only from males, females, and brood from Argentina. *Pseudoatta* resembles

*Acromyrmex* and may have evolved from it. Gallardo's description was based on three dealate females and one male, each from a different locality. Bruch recorded two nests of *A. lundii* at the cities of Rosario and La Plata from which the sexual castes of *Pseudoatta* emerged almost daily from April 27 to May 20, 1924. Only workers of *lundii* were present in the nest, and no queen of the host species could be found. The brood was that of *Pseudoatta*. This remarkable state of affairs has not been investigated further.

(12) *Atta* (14 species) (figs. 22, 27-30, 41, 42, 46, 48, 49, 50):

The most recent publications on the taxonomy and distribution of *Atta* are by Borgmeier (1950,

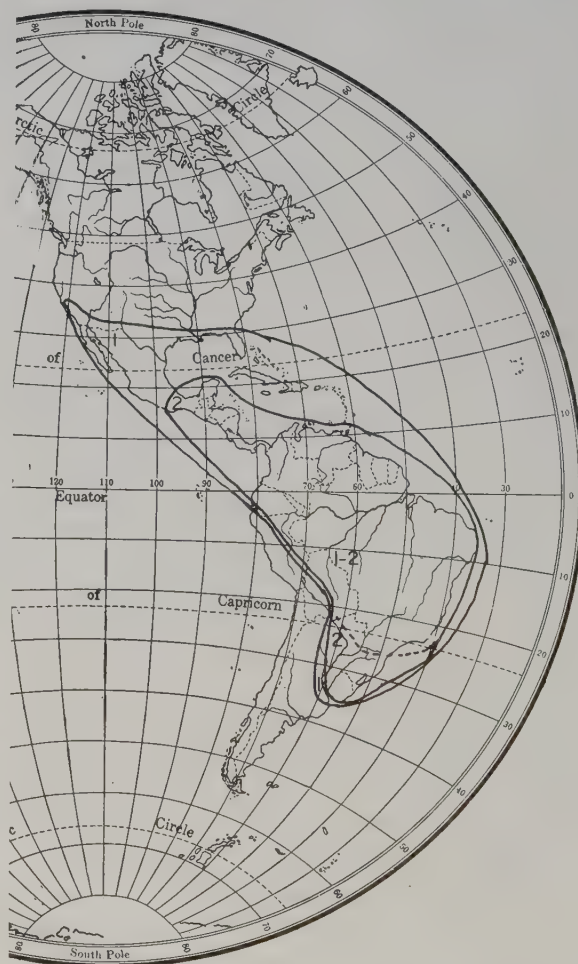


FIG. 44. The approximate distribution of *Cyphomyrmex* (1) and *Sericomyrmex*, *Myrmicocrypta* and *Apterostigma* (2), that of *Sericomyrmex* in the south extending to the dotted line.



1959), Gonçalves (1942, 1960), and Weber (1968, 1969). The northernmost species are *A. insularis*, (Cuba) *texana* (United States) and *mexicana* (Mexico). Several of the other species are primarily Brazilian, and distribution maps for them have been published by Gonçalves (1960). *Atta* is the only genus with soldiers; these large individuals do not develop until colonies are six or seven months to two years old. *Atta* has the largest colonies and does the most conspicuous damage to vegetation of all fungus-growers. It probably evolved from *Acromyrmex* or its antecedents.

#### DISTRIBUTION AND MIGRATION OF GARDENING ANTS

The present distribution of the fungus-growers is entirely American (fig. 43) (see appendix for



FIG. 45. Approximate distribution of *Mycetosoritis* (1), *Mycocepurus* (2), *Mycetarotes* (3).

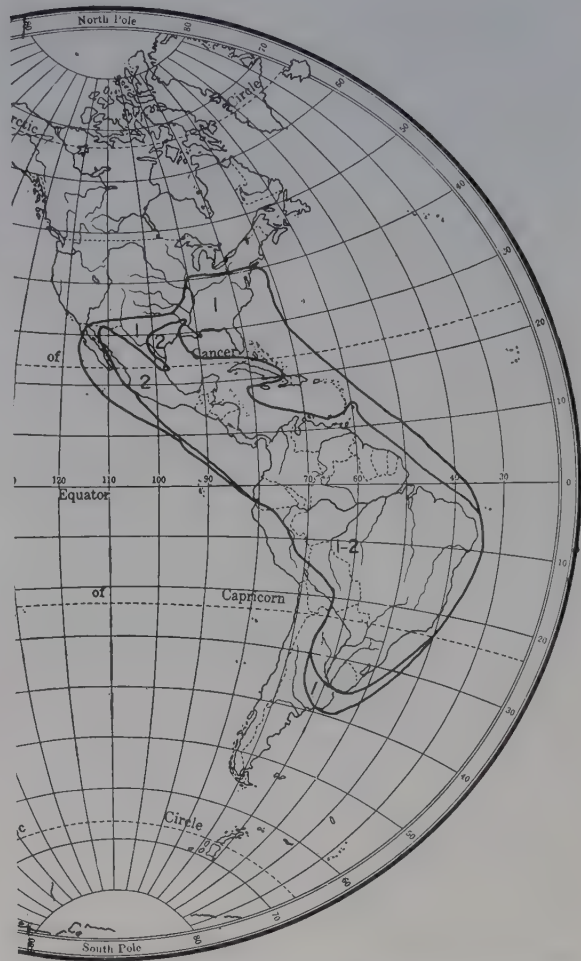


FIG. 46. Distribution of *Trachymyrmex* (1) and *Atta* (2), the western boundaries being incompletely known.

northern species) and they probably originated in the moist lowland tropics of northern South America where the climate has been warm and stable since the Tertiary Period. The attines may have evolved from harvester ants that collect seeds and other pieces of vegetation on which the adult and larval ants feed directly. Some of these harvesters such as *Pogonomyrmex occidentalis* cut seeds from standing plants, collect insect feces, and store them in nests where fungi will grow on the food if it becomes too moist. The primitive fungus-growing ants probably collected feces and pieces of vegetation before they acquired the habit of cutting living plants (Weber, 1958).

Parts of South America from sea level to 200 meters elevation may well have been warm and humid enough to permit the ants and their

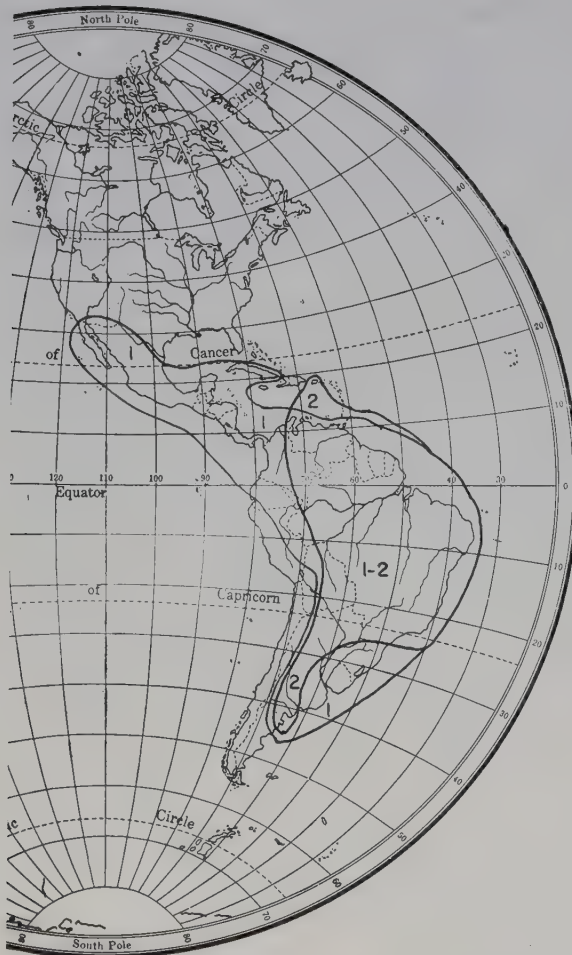


FIG. 47. Distribution of *Acromyrmex* (1) and *Mycetophylax* (2), the western boundaries being incompletely known.

fungi to survive when climatic changes were severe outside the tropics. The largest area of tropical South America at present no more than 200 meters above sea level is the Amazonian basin. This basin is connected with the Orinoco basin below 200 meters elevation by the narrow Casiquiare channel in the interior and more broadly along the Atlantic coast. The third great South American low-lying river basin is that of the Rio Paraná which has no such connection with the Amazon. It is, however, connected by somewhat higher (below 500 meters) swampy land along the eastern Bolivian border.

There were apparently ample opportunities for fungus-growing ants to migrate south into Argentina where they have developed greater resistance to low temperature (see pp. 64 and 71) than in

North America. While moving south, the ants probably simultaneously adapted to the drier conditions of the grassland, llanos, and pampas as well as to the colder winter temperatures of southern South America. At present the fungus-growers have reached Latitude  $44^{\circ}$  South, in the Province of Chubut, Argentina. This southern boundary has probably fluctuated markedly with climatic variations over the millennia. Only small species adapted to semi desert conditions are found there today. *Atta* does not now quite reach the Province of Buenos Aires but comes close at the present time at Latitude  $33^{\circ}$  in neighboring areas, including Uruguay, and may well be in the process of moving south. Evidence based



FIG. 48. Approximate distribution of six species of *Atta* (Brazilian distribution after Gonçalves, 1960, and Amante, 1967). (1) *texana*; (2) *mexicana*; (3) *insularis*; (4) *laevigata*; (5) *capiguara*; (6) *vollenweideri*.



on their morphology and behavior suggests that smaller genera must have appeared much earlier and have had time to make the necessary adjustments to temperate zone life.

A curious fact is that the ants are not known from the entire country of Chile. Evidently they could not invade the desertic coast from the north nor could they cross the Andes from the east, where many species are found at the same latitudes in Argentina. Habitats in Chile, especially gardens and plantations, must be suitable for some attines if they become introduced.

From northern South America the ants now have 200-meter or lower routes into and through Central America into Mexico. The Isthmian connection was broken a number of times, and



FIG. 49. Approximate areas occupied by *Atta bisphaerica* Forel (1), *goiana* Gonçalves (2), *opaciceps* Borgmeier (3), and *robusta* Borgmeier (after Amante, 1970, personal communication).



FIG. 50. Approximate distribution of the two most important *Atta*, (1) *cephalotes* and (2) *sexdens* (Brazilian distribution after Gonçalves, 1960).

resulting geographical isolation probably encouraged the development of the rich Central American fauna. The peninsula of Yucatan lies at 200 meters or lower and is connected with the United States along the Gulf of Mexico by a narrow zone of similar lowland. It may also have been the pathway to Cuba, where *Atta insularis* may have evolved from the ancestors of *texana* and *mexicana*. The west coast of Mexico is less favorable for migrations of tropical ants but does have a narrow belt of land under 200 meters along the coast continuous with Lower California and California.

The ants invaded North America, presumably in several waves, but must have been exterminated along the East Coast during the Pleistocene. One species, *Trachymyrmex septentrion-*



*alis*, was taken on Long Island, New York (40° 50' N. Lat.) early in this century and is presently found in the New Jersey Pine Barrens. There it can only be active about five months (May to September) during most years and rarely approaches six-months activity in the warmest years. *T. septentrionalis* also goes up the Mississippi valley to 40° 22' N. Lat. in Illinois (Weber, 1970). Another species, *Acromyrmex* (*M.*) *versicolor*, adapted to live in deserts, has reached the Mohave Desert in Southern California and *Cyphomyrmex wheeleri*, found at Merced, California (37° 20' N. Lat.), is the most northern known attine on the West Coast. Although most species of attines are found in lowland moist tropical forests, many of these areas are adjacent to forested mountains. The highest elevation at which any attine has been found is 3,500 meters for *Acromyrmex* (*M.*) *striatus* in the Andes of Argentina. Three other species, *A. bruchi*, *A. lundii corallina*, and *A. lobicornis* are recorded from Argentina at 3,100 meters. *Acromyrmex* also extends up to 2,300–3,000 meters in Colombia, Ecuador, and Bolivia. *Atta* does not extend as high, with the maximum elevation about 2,000 meters in Colombia and Mexico. I have collected *Cyphomyrmex rimosus*, *Apterostigma mayri*, and *Atta cephalotes opaca* at 1,900 meters' elevation at Medellín, Colombia, an unusually high elevation for them.

The seldom-collected *Acromyrmex ambiguus* of the pampas of Buenos Aires Province, Argentina appears to fluctuate in abundance and distribution according to my limited observations in 1960–1962. Exact sites where the ants nested in the 1961 winter were free of this species the next winter, the common *Acromyrmex lundii* being abundant in the same area throughout the period.

A century ago, F. Smith (1868) recorded that, in the Minas district of Brazil, *Atta sexdens* was not known as a pest in 1848 except by name. His correspondent reported that the species gradually advanced across the country and in the 1850's reached the Organ Mountains. *Atta capiguara*, described in 1944 from São Paulo, Brazil, has recently been recognized as a major pest of pastures and may have spread in recent years from a more limited distribution (Amante, 1967b).

Changes in *Atta* distribution in the Isthmus of Panama have recently been summarized (Weber, 1969b). Between 1938 and 1966 the

common *Atta cephalotes isthmicola* and *Atta colombica tonsipes* of Barro Colorado Island, in the Panama Canal Zone, have fluctuated in their distribution at known locations along marked island paths. The latter species and *Atta sexdens* of the Pacific drainage have also fluctuated. *Atta sexdens* is a grassland species, whereas *A. tonsipes* is primarily of the forest. At the time of the arrival of the Europeans, the Indians had increased to perhaps one million people and had reduced the forest by fires and agriculture. This must have permitted *sexdens* to occupy much of the Pacific slope of the isthmus as the grasslands increased in extent. With the rapid decrease in Indian population following the European conquest, the grasslands became partly overgrown with forest and *tonsipes* must have invaded the former *sexdens* territory. At the present time grasslands are again becoming more extensive as human populations are growing.

In 1945 *Atta vollenweideri* was recorded from the city of Tucumán, Argentina, but a few years later it disappeared. In 1949–1950 it could still be found some kilometers to the north but it then disappeared there. Kusnezov (1953) conjectured that the cause of the latter was a prolonged winter drought in 1950.

The appearance of *Atta cephalotes* in Bahia, Brazil (fig. 50), many hundreds of kilometers from its Amazonian range, evidently took place in the 1930's (P. Silva, pers. commun.).

A recent review of West Indian distribution of *Acromyrmex octospinosus* (Cherrett, 1968c) shows that, in addition to Cuba, Trinidad, and Tobago that have long had the species, it has in recent years been found on Curaçao and Guadeloupe. On Guadeloupe the species was discovered in 1954 and considered to have been a human importation of a few years previously. In 1968 it occupied an area of about 5 × 6 km. and is thought to be spreading.

The areas occupied by other species of Attini will probably be shown to vary more from time to time than is generally thought to be the case. Distributions will be influenced by fluctuations in weather and interrelated factors such as changes in the survival of females or young colonies (see chapter 5) and changes in the substrate plants over a large area. It would be a worth-while effort to map the locations of mature *Atta* nests in all natural reserves in the Americas for future generations to follow.

## 4. MATING AND ESTABLISHMENT OF COLONIES

### FLIGHTS OF REPRODUCTIVE CASTES

The attines and most other ants have flights of males and females from the parent colonies that serve to disperse the ants and result in fertilization of the females. Sometimes the reproductives leave the parent colonies by the thousands, and the flights have been called "swarms" or "swarming." Since mating normally occurs in the air, it is appropriate to refer to the flights as mating or nuptial flights. However, in *Pseudoeatta* some mating apparently takes place within the parent colony or at the entrance before the females take flight.

The flights usually occur during a limited season of the year favorable for the survival of the young queens and their new colonies. In most tropical areas the onset of the rainy season probably triggers the nuptial flights, thereby synchronizing flights from different colonies and increasing the chances for cross-fertilization. At the beginning of the rainy season the surface soil will be moist and most easily penetrated, and the humidity will be high enough to facilitate survival of the delicate fungus. In the South and North Temperate Zones mating flights occur during the summer and may also be synchronized by rains. Little is known about the exact factors influencing the flights of even the most common or important species of attines. The sexual forms may remain in the nest chambers for weeks after they have matured and may collect in superficial chambers or tunnels.

Although weather conditions clearly play a role in synchronizing flights, some nests in an area may have reproductives that do not participate. Other mating flights may consist of a few scattered individuals leaving singly or a few at a time.

### FLIGHTS OF MAJOR GENERA

#### *Trachymyrmex*, *Acromyrmex* and *Atta*

The vast ranges of the three chief genera: *Trachymyrmex*, *Acromyrmex*, and *Atta* (figs. 46, 47-50) encompass all of the major habitats of the gardening ants and in one area flights may be taking place when the ants may be completely inactive in another area. There are flights in some region every month of the year. When

flights are taking place in the United States the sexes are inactive in Argentina and vice versa.

#### *Trachymyrmex*:

Most records are for the northernmost species, *septentrionalis*. Cole (1939) collected the winged sexes from Mississippi nests after June 11 and observed mating flights from July 8 to the middle of August. When the nest would be opened before the mating flight both sexes would fly a few inches at a time before hurrying for cover. By June 24 my Florida records show nuptial flights taking place in the morning. By noon the females, wings gone, were scurrying about looking for a site in sandy soil to dig in. They were then unusually quick and elusive compared with their behavior at other times and would quickly take refuge under pine needles and other leaves on the sand surface. On June 26 there was similar activity and one female at 8:30 A.M. was carrying a pellet of ant garden with hyphae between her mandibles.

Winged females emerged from nests in New Jersey on September 4. The temperature in the shade at 3:12 P.M. was 30.8° C at a height of 100 cm. and 32° C on the ground. It was calm or with a faint breeze and the sky was mostly clear. The females emerged from an inconspicuous entrance in bare sand. Workers accompanied the females to the entrance and neither caste appeared agitated. The females climbed low, scrubby vegetation and took flight singly. They flew slowly at a height of several meters in the calm air, and finally several flew to the top of a nearby pine tree about 8 meters high. They appeared to fly around the top of the tree as other ants do on their nuptial flight, then descended. The emergence from the nest took place from 3:12 to 3:24 P.M. and by 4:30 P.M. a number, now dealated, were excavating in the nearby sandy soil.

Moser (1963) observed the latter part of a flight of this species near Gardner, Louisiana, on July 4. This took place in the early afternoon when the temperature was about 31.5° C and the relative humidity 44-48 per cent. A rain of 17 mm. had fallen the preceding afternoon. The winged ants crawled up vegetation and took flight as in the New Jersey case. Mating was



not observed. By 2:15 P.M. the flight appeared to be over. He has also seen wingless females on the ground from June 20 to September 3.

Flights of males of a five-year-old laboratory colony of *Trachymyrmex zeteki* took place in April and May, 1959, and in April, 1960 (Weber, 1964). The ants took short jumps of one to 8 centimeters up in the air of a confined space 11 cm. high, 14 cm. wide and 15–20 cm. deep. Their flights horizontally were up to 10 cm. in length. The ants rose on their fore legs, when taking flight, so that the body was at an angle. They expanded their wings and then jumped with the wings vibrating and took flight. The apex of the gaster would touch the floor while the head and wings were raised. This method in nature would be appropriate for taking flight from leaves or twigs on the forest floor. All males that were produced were collected and totalled 44 in the two broods.

Mating flights of *T. urichi* took place in Trinidad on July 1 (Weber, 1967). The first seen was a female flying at 6:50 A.M. when it was calm and clear in a bright sun. The next minute others were seen dealated, crawling on the patio of a house, and more were seen in the next half hour. Others were flying or had just descended, including a female that ruffed her wings as recorded in other genera. There was no evidence of a mass flight of *urichi* or of *Acromyrmex octospinosus*, which was taking place at the same time and place. Males of both were taken in flight and scattered on the ground until 8:45 A.M., as were the females. A light sprinkle of rain fell at 8:10 A.M.

A rain of 40 mm. took place the previous day and by 1:30 P.M. of July 1 there was an additional 10 mm. The temperature at the surface of the grass on July 1 at 8–8:10 A.M. over which sexes of both species were flying and descending was 31°C in the sun and 27.5° in the shade.

Flights of *T. tucumanus* in Argentina (Kusnezov, 1962) and *wheeleri* in Colombia (Weber, 1958) took place at 7–11 P.M. and 3–4 A.M., respectively.

Maximum male activity was reached in a captive colony of *Trachymyrmex septentrionalis* collected in New Jersey on June 29. By mid-July it had a brood of sexual pupae, including female, starting to emerge as adults on July 23 and males emerged on July 26. During August this brood stayed mostly in the darkened chamber containing the fungus garden. The nest was moved to another room and placed on a shelf

near the single window facing east. A black shade kept the room dark until it was raised in the morning about 9 A.M. The empty feeding chamber was exposed toward the light and it was here that all attempts to fly took place. The ants had to pass through a narrow entrance to reach the empty chamber from the permanently darkened chamber with the garden (fig. 134). Both males and females ran about erratically, often jumped short distances, and tried to fly, but no copulation was attempted.

This activity started in late August and reached its peak at the end of September and early October. No attempts at swarming took place in the morning. During September the males emerged about 3 P.M. although the room had been lighted all morning. The swarming activity increased in tempo to the end of the hour and frequently after 4 P.M. During the last week they continued until after 5 P.M. on three consecutive days, the latest activity noted being 5:45 P.M. on September 25. Temperatures at the swarming site were 22–23° C and the outdoor weather variably clear to cloudy with no apparent correlation with activity.

Male activity reached a maximum during October at about 4:30–5:30 P.M., extending as late as 6:15 P.M. on October 18. They were dying by late October and were removed to the lighted chamber by the workers if they did not die there.

A few surviving in November were clearly enfeebled and might wander about in the lighted chamber in the afternoon. The usual swarming behavior was noted as early as 2:10 P.M. on November 4 with maximum activity to 3:38 P.M.; by 4:50 all had returned to the fungus garden.

In following years the male activity was similar. All swarming activity started in August and by early September became a well-defined pattern. The room was normally lighted from a single window on the east and activity was directed towards it, regardless of the sunniness or cloudiness of the day, whether it was raining or clear and whether it was cold outside or warm. The temperature was maintained at 24–26° C.

As before, there was no swarming until the afternoon. In September the major activity came between 3 and 4 P.M., in October between 2 and 4 P.M. and in November mostly between 1 and 3 P.M., probably with increasing shortness of the day. Males in other colonies performed similarly in other rooms at the same times, despite the variability of room lighting.



The males in a windowless basement room, provided the time was in mid-afternoon, would also start running about after five minutes exposure to artificial light, as they were active at the same time in sister colonies in the upstairs lighted room.

These mature males, like those of other gardening ants, are capable of feeding by themselves on the fungus in the garden and may also accept food by regurgitation from workers.

#### *Acromyrmex*:

Perhaps the best documented nuptial flights in the widespread genus *Acromyrmex* are those for the economically important and common Argentine species, *lundi*.

Kusnezov (1962) recorded the flight dates and proportion of sexes involved at Tucumán (26–27° C Lat.) in northwest Argentina.

Date	Females	Males
October 15, 1948	124	110
October 30, 1950	1254	1576
November 14, 1950	825	2683
October 25, 1952	751	2315
November 13, 1952	5003	5561
	7957	12,245

In 1954 he observed flights on October 5 and November 2, 9, and 11. In 1956 the dates were October 8 and 17; November 1, 6, 22 and December 12. There was a diminished flight on January 22, 1959.

During a two-year residence in suburban Buenos Aires (34° S. Lat.) in Argentina I recorded the dates for the flights of the same species at my garden. Flights took place on November 23 and December 17, 1960, and seven times in 1961 (October 12, 22, and 29; November 2, 11, and 14; December 17). A flight also took place across the broad estuary of the Río de la Plata at Carrasco, suburb of Montevideo, Uruguay, on December 11. Many ants fell in the river and drowned.

All flights took place in the mornings when the weather in this temperate zone area was considered to be tropical, warm, and humid. Representative meteorological data for the October and November, 1961, flights may be summarized as follows:

Previous day: warming with rising humidity  
Flight day: 18.5–21.7° C from 6:50 A.M. to 9:30 A.M.  
93–64 per cent relative humidity to 9:30 A.M.

755–756 atmospheric pressure in mm.  
weather calm with sky mostly clear  
6:50–10:30 A.M.-bulk of flight

The sexes crawled over the same areas of the ground or pavement without showing any reaction to one another. They would then crawl singly up grass blades, bushes, or a wooden railing. None was seen to leave from a flat surface. The sexes would vibrate their wings, then take flight. They flew off into the calm air in a weak spiral and tended at this site to drift towards the sun and river (Río de la Plata). Pairing took place in the air. The parental nests in the meanwhile had been disgorging workers in great numbers that milled about agitatedly on flat surfaces. Mated females descended quickly from the flights and lost their wings within minutes so that during a flight there would be dealate females quickly running about seeking shelter in the same area. Some pairing may have been completed on the ground before the females lost their wings. When the sexes were placed in separate vials of alcohol for study both stridulated loudly enough to be heard easily. The males stridulated longer and louder.

The December 17, 1961 flights of the *lundi* sexes took place in my house about 10 A.M. The room temperature at the time was 22° C and the outside shade temperature about 24° C. The morning was sunny and calm and it was known for the past year that these ants were living under the house. The emergence took place from a small crack 4 by 11 millimeters in diameter in the doorway between two rooms. At 10 A.M. they were coming up in large numbers, accompanied by many workers, particularly of the smallest sizes. All of these were crawling up the frame of the door to its entire height. Occasionally males and females would then fly from the frame to a large picture window across one room on the sunny side, where they were attracted by the daylight. The flights lasted for about an hour and during this period some of the winged ones, particularly females, went back into the hole in the flooring as did nearly all of the workers.

Copulation of the sexes took place by the smaller male riding on the back of the female, with the apex of his gaster turned down and the genitalia of the two interlocked. His head was directed forward and at a level with her epinotum. The union lasted about one-half a minute in one case and the ants disengaged readily; in

another pair it took one and one-half minutes. When the two came apart as they were placed in a test tube the male attempted to unite again. The males had considerable flexibility to their abdominal segments and often attempted to engage the female genitalia repeatedly by twisting about. Mostly the attempts were unsuccessful at first. Several males might ride on one female as she ran about. By 11:50 A.M. most of the sexual activity had ceased. All the females free in the rooms at noon still retained their wings.

The July 1 flight of *Acromyrmex octospinosus* was noted above with *Trachymyrmex urichi*. The first females of the *Acromyrmex* were already wingless when seen at 7:30 A.M. and the last were taken at 10:45 A.M. Three of these females developed colonies that thrived for more than six years in the laboratory.

Wheeler (1917) described the nuptial flight for *Acromyrmex* (*Moellerius*) *versicolor* in Arizona. The flight was taking place at 5:50 A.M. in calm, clear air on July 30, when first seen, after a heavy rain of the day before. The ants were in numerous sharply defined swarms, elliptical or egg-shaped and 2 to 3 meters tall by one or slightly more meters in breadth, and stationary at a height of 6 to 9 meters. The swarms were 12 to 15 meters apart in some places but more commonly were separated by a distance of 30–90 meters. Similar swarms were visible over the level desert as far as the eye could see. (This was similar to the swarming of an unrelated ant, *Araucomyrmex tener* Mayr, on the east slopes of the Andes in Argentina [Weber, 1963]).

The ants were in zigzag motion and constantly receiving single males and females flying straight to it from a distance. The swarm did not increase in size, however, because pairs of ants in copula were constantly raining down to the ground from the lower part of the mass. A writhing and struggling layer of ants often a meter in diameter was under each swarm. A swarm was above a puddle of water in one case and the surface became black with the fallen pairs. The Wheeler party rode for fully half an hour through these swarms.

This method had been observed by Amante (pers. commun.) for *A. landolti* in São Paulo, Brazil. The females flew into the swarm of males, males attached themselves and the pairs fell to the ground. The female sometimes returned to the swarm after detachment for another mating.

#### *Atta*:

One of the best places to see the *Atta* flights is the state of São Paulo, Brazil. An ant of the grasslands here, *capiguara*, has been intensively examined by Amante (1966–1968) from the point of view of control. Rains are prerequisite to the flights and temperatures must be above 20° C. A cold wind coming in the early stages of a flight will cause the sexes to return to the nest. The hours for flight are variable and nearby colonies may not be involved when certain nests are having their flights. The sexes fly so high that they can barely be seen but their stridulation can be heard as a buzzing sound. Three species in one area here may have their flights at about the same time but do not intermingle. These are *sexdens* subspecies *rubropilosa* and *laevigata*.

The nuptial flight of *Atta texana* was reported by Walter, Seaton and Mathewson (1938) to take place early on clear, moonless nights in May or June at San Antonio, Texas. Preliminary to this, from mid-April to June, the entrances to the nests were enlarged to two or three times normal size. A few young females might appear at the entrances soon after dark and then the males about a half hour later. They would stay near the entrances, then return to the deeper parts of the nest and be replaced by others. By about midnight all sexual forms had disappeared into the nest and the workers had stopped up the entrances with trash. The only actual flight was recorded as taking place about 9 P.M., when great numbers struck the side of a house.

Moser (1967) observed more than 50 flights of *texana* from about 20 nests in Louisiana. The sexes move to the upper nest chambers prior to flying and may remain there for one or two months. The ratio of females to males in the chambers varied and in 1961 there were 875 females to 1,080 males in 26 cavities. The sexes would start moving to the outer surface of the nest shortly after dark (8 P.M.) and by midnight as many as 2,000 would be out. By 3:30 A.M. there would be 5,000 or more. Flights were always preceded by a rain sufficient to wet the nest surface and relative humidity of 98–100 per cent. If rain was heavy the sexes from a particular nest would emerge on three of four successive nights. The sexes flew as early as 3:30 A.M. and as late as 4:15 A.M., the ants flying one or a few at a time at first, then a major exodus takes place, the ants taking flight directly from the ground. The minimum temperature



for the flight appears to be 16°C. Moser was able to predict the time of flight by the irritable behavior of the workers, the ants running about and attacking living and dead objects in their path. Mating was not observed.

Mitchell and Pierce (1911) referred to a large number of winged *Atta texana* in May, 1892, passing along the main street of Victoria, Texas, in a swarm about 30 feet long and over eight feet wide. The ants flew in a zigzag manner for two blocks and then dispersed singly. Another time a swarm was observed on a river, floating alive in a mass about two feet across, as in *Acromyrmex lundii* above.

#### MATING FLIGHTS OF OTHER GENERA OF ATTINI

Only the ant specialist is likely to observe and identify the small sexual forms of other genera. The observations are scattered and are my unpublished records unless otherwise specified.

##### *Cyphomyrmex*:

Males of *C. rimosus* were observed in a mating aggregation at 3 P.M. in bright sunlight on May 11 in Trinidad. Rain had fallen the preceding day and night, and the afternoon was hot and humid. The males were flying in a zigzag manner at a height of 2.5–3.0 meters and concentrated around my head. An alate female in a study nest attempted flight on March 30 at 5:35 P.M. when the sun momentarily struck the nest. Males showed agitation preparatory to a flight on April 16. Males of the subspecies *trinitatis* took flight when a Guyana nest was exposed on August 21.

Males in observation nests of the Panamanian *C. costatus* and the Guyana *C. bigibbosus* attempted to fly briefly on single occasions.

Kusnezov (1962) took 8 females and 107 males from a flight of *Cyphomyrmex nemei* on February 17. A flight of *rimosus* on December 1 consisted of 3 females and 35 males and one of *quebradae* on this day had three females and four males.

##### *Mycetophylax*:

Males of *M. conformis* in observation nests indicated their readiness to fly in Trinidad in late March and early April. The males ran about in observation nests during afternoons in October and November, remaining quietly in the gardens at other times of the day. Bruch (1923) reported *M. emeryi arenicola* sexes flying during the mornings in late December and early Jan-

uary in Argentina. Kusnezov (1962) found that the Argentine flights took place in November to February only when the sun was low and the sky clear, both in the morning and afternoon. Mating takes place in the air, the pairs later falling to the ground.

##### *Mycocepurus*:

Kempf (1963) reported mating flights of *goeldii* taking place in south Brazil during the daytime from October to February, copulation taking place on the ground. Kerr (1961) recorded a flight of *M. goeldii* in Brazil on October 17 in the morning in which there were 12.5 males to each female (150 to 12). Individual females were seen copulating with up to four males. He observed males of *smithi* flying at the same time and place. A winged female of *smithi* from a flight alighted on my arm in Trinidad on June 22 at 3:50 P.M.

##### *Mycetarotes*:

Kusnezov (1962) recorded an unidentified species of this genus (probably *parallelus*) flying November to January in Argentina.

##### *Myrmicocrypta*:

Males of a Trinidad colony of *Myrmicocrypta buenzlii* collected in March showed readiness to fly on August 8 in an observation nest. A female alighted on my arm at 10 A.M. on June 8 in Trinidad.

##### *Apterostigma*:

Kusnezov (1962) recorded an unidentified species (perhaps *steigeri*) flying October to January in Argentina and I took *steigeri* sexes here on October 12 in the morning and on the twenty-ninth at 10 A.M. to 2 P.M. It was clear but humid and rain fell later in the day. The sexes flew singly.

##### *Sericomyrmex*:

On June 29 along the Oko River, Guyana at 8:30 A.M. males of *Sericomyrmex* sp. were alighting on leaves and clothes in overcast weather with rain imminent. On July 20 they were flying near the Oronoque River, Guyana at 6:00 A.M., also in overcast weather following a night rain. A laboratory nest of *S. urichi* had male broods that flew or ran about for several days each in May through September, then died



shortly thereafter in each of three years (see chapter 6). In two of the years the total male to female production was 666 to 372 and 3,888 to 1, respectively. Another nest had males that took short flights repeatedly in afternoons in April and May. Females indicated readiness to fly in another captive colony on January 12 and had matured five or six weeks earlier.

#### *Comparison of Mating Flights of Different Genera*

The data, limited as they are, indicate a considerable regularity in flight time according to genus and species. The small and primitive species probably are diurnal in flying and, since they are mostly forest species, the flights go unnoticed. The common northern *Trachymyrmex septentrionalis* is an afternoon flyer in New Jersey but a morning flyer in Florida. The species *urichi* of Trinidad flies in the morning. The desert *Acromyrmex (M.) versicolor* flies at dawn, thus giving several precious hours to dig into the soil before the fierce midday heat. Both the tropical *Acromyrmex octospinosus* and the Argentine temperate zone *A. lundii* fly early in the morning.

The Colombian *T. wheeleri* may fly at night in the Andes while the subtropical Argentine *T. tucumanus* flies in the early night. The day-flying *Atta* species of subtropical south Brazil contrast with the late night or early dawn flying *texana* of the United States. Limited evidence suggests that the common tropical *Atta sexdens* and *cephalotes* may also be night-flyers.

A species that flies at night may escape many enemies that prey on the day-flyers. If, however, the flights are widely dispersed and the ants are extremely abundant, as they are in south Brazil, the survival of some is assured.

#### *Survival of the Males and Females*

The males in nature die on the day of the mating flight. If they have only appeared at the nest entrances they can return and are accepted by the workers, but once they take flight there is no evidence that they can return. This is also true so far as known of the females, although in one example (Weber, 1941) a colony of *Cyphomyrmex rimosus* on the beach of the Bay of Panama contained such a high proportion of dealated females to workers (44 to 174) as to indicate that most had returned to the parental nest. The nest was in an isolated rotted twig just above high-tide level and the prevailing

winds blew off the land. The previous month had been one of record rainfall with several rains each day. The females may have been driven down to the beach by wind and rain during the mating flight and had no other suitable refuges nearby.

In the normal situation the females of attines descend randomly over a wide area but sometimes there will be a few that tunnel into the soil within several centimeters of each other. This is as true of *Atta* as of the small species (fig. 52).

While in flight the ants may be seized by predators (see chapter 9, p. 119) and this is only the first of their hazards. Autuori (1950) concluded that in *Atta sexdens rubropilosa* fully 99.95 per cent of the females in a flight fail to found successful colonies and the remaining 0.05 per cent is more than sufficient to maintain a continuous agricultural hazard. Walter *et al.* (1938) noted a mass of dead *Atta texana* against a house as having at a distance the size and appearance of the disintegrated carcass of a small red calf. The record above of a flight of *Acromyrmex lundii* fallen in the estuary of a river illustrates another hazard. There may have been no survivors to this flight of many thousands since they were being washed ashore on a clear sandy beach in sunlight where the sun and heat would kill them quickly before they could crawl off the bare beach to suitable grassy areas.

#### ESTABLISHMENT OF COLONIES

The events following the descent of the female to the establishment of successful young colonies are included here.

#### LOSS OF WINGS BY THE FEMALE

Loss of wings is necessary. To retain the wings in the first place would introduce a hazard and an impediment when digging into the soil, closing the entrance to the cell, and moving about on the developing garden. Early in a morning nuptial flight there will be both winged and wingless females found on the ground, the wingless having already been fertilized. The winged and unfertilized females do not normally dig into the soil. The conventional expression of dropping the wings is inexact. The females of gardening ants markedly facilitate this process of losing the wings.

Females of *Acromyrmex lundii*, immediately upon falling to the ground after their dissemina-

tion flight, were observed in Buenos Aires to run about through short grass in an agitated manner, rubbing the wings against the grass as they went. The wing may also be turned at an angle to start the detachment. It was quickly brushed off in this manner and normally breaks off easily at the base. Females that were captured and isolated in test tubes before they could lose their wings held on to them for several days or weeks. They often stroked them with the legs but this was insufficient to break them off and they were probably unfertilized.

Females of *Trachymyrmex septentrionalis* could be seen more precisely under the microscope to take positive action. They used the hind legs not only to rub the wings but tightly flexed the leg so that the wing was held as in a vise. A female would stand still, then rub either the fore or hind wing while turning it at a marked angle. The fore wing was of a size that the cramped hind leg could hold it for many seconds, the leg moving the wing down and holding it there in an apparent effort by the ant to pull or break it off. Wings under these conditions were removed irregularly in respect to fore or hind or right or left. Commonly during the transition period the small hind wing would be turned at an angle for a day or more. A female of *T. urichi*, freshly descended from her nuptial flight, was seen to ruffle her wings exactly as in *Acromyrmex lundii*.

The female of *Atta texana* breaks off her wings in the same manner (Moser, 1967). The wing is extended at right angles to the body and is broken off by the movement of a leg against it. Blowing air on unfertilized females induced them to remove their wings.

#### ORIGIN OF THE QUEEN'S NEW GARDEN

A basic feature of the gardening ants is their handing down of the nucleus of the fungus garden from one generation to the next by way of the females on their mating flight. This is accomplished by their retaining bits of the parental nest fungus in their infrabuccal pocket, described in chapter 2. The discovery by v. Ihering (1898) that the female of *Atta sexdens* carries this as a 0.6 mm. mass was reviewed and carried further by Huber (1905) as described in chapter 5. Studies of this type were expanded by Bruch (1921) and Autuori (1942-1956) and have been fully verified since.

Three females of *Trachymyrmex septentrionalis* from their New Jersey mating flight (Weber,

1962) were collected and isolated in small containers with moist, clean white quartz sand. Each had by the next day a small pellet of fungus garden sprouting thin, white hyphae. The pellet must have come from the contents of the infrabuccal pocket since the females had been carefully examined and did not have any fragment of a garden between their mandibles. Moreover, queens dig their initial nests and would not be able to hold a pellet of fungus in their mandibles, but it is apparently well protected in the infrabuccal pocket.

After the November 14, 1961, mating flights of *Acromyrmex lundii* described earlier, I isolated a number of females in several types of containers with earth. They were captured an hour or two after flights and soon after losing their wings. A high proportion of successful beginning fungus gardens resulted.

In one case 7 females were placed in one glass jar of earth and they cooperated by placing their individual gardens in a cluster attached to the glass ceiling plate. The general pattern in other cases at this time was to start the garden by expelling the contents of the infrabuccal pocket,



FIG. 51. The earliest stage in the formation of a colony of *Acromyrmex octospinosus* in a shell vial. The female is at the left and her incipient garden consisting of the contents of her infrabuccal pocket and sprouting ant hyphae at the right above her bent right leg. The first eggs will be laid on this garden. Trinidad.





FIG. 52. Craters of early stages of *Atta colombica tonsipes* nests created by first broods of the queens. Each crater marks the site where a female dug into the ground after her mating flight. Ruler 15 cm. long. Panama.

then immediately lay eggs on it. Not all eggs were laid on this garden and some were stuck to the ceiling or side of the container. The original nucleus for the garden must have been in the infrabuccal pocket since no pieces of garden from the parental nest could be detected between the mandibles of the freshly captured females or even before capture, although I scrutinized them carefully.

The success of the *lundi* females in starting a new garden and colony was much higher when they were captured within an hour or two after the flight, than when they were captured more hours or days later. Either these females did not have viable bits of fungus or for some reason the initial garden was damaged and did not survive.

Isolated females of *Trachymyrmex urichi* and *Acromyrmex octospinosus* from Trinidad nuptial flights successfully started new colonies (Weber, 1967b) (fig. 51). In all cases they were examined carefully to make sure that they were not carrying parts of the parental garden between their mandibles. They were then placed in individual containers. They would regurgitate the contents of the infrabuccal pocket within hours of

capture and the new garden would be sprouting hyphae the next day. Of six isolated *Acromyrmex* females, five started gardens. The most successful had a garden of about 2 mm. diameter on the fourth day. Within two weeks from capture she had a garden  $6 \times 7$  mm. with several small masses of inflated hyphae (staphylae).

#### STARTING THE NEST AND GARDEN

The females start to dig into the soil close to the site where they lost their wings. They move quickly about in a zigzag or erratic manner and may sometimes find a fallen leaf or twig under which they start to dig but commonly in *Acromyrmex* and *Atta* the site is the fully exposed soil surface (figs. 52, 115). It is not necessary for them to find a crevice in the soil. Each female commonly works by herself at her own site although two *Atta cephalotes* females in captivity did temporarily cooperate (Weber, 1937). A female, to be successful as noted above, must carry a bit of the parental fungus garden mycelium in her infrabuccal pocket (fig. 10). A marked difference compared with termites is that the male plays no role in digging the initial chamber. She would not have left the parental nest in the first place had the outside air not been humid and the ground wet or at least damp. This makes a great deal of difference in lessening the hazard of transferring the bit of the fungus in the pocket to the soil chamber she will soon have to dig. Moist soil is also easier to dig in and does not collapse.

My evidence with species in various genera is that some of the females on the nuptial flight either do not have a viable bit of the fungus from the parental garden or they lose it before they can get it safely underground. For example, of some 30 *Trachymyrmex urichi* from a nuptial flight, 20 started gardens. None had had any bits of the parental garden between the mandibles, when they were isolated separately (Weber, 1967b). Time is also of the essence if the females come down in poor places and cannot dig in fast enough to escape predators and desiccation.

It is not unusual to pick up females running about after the nuptial flight and, after isolating them, to find that they will lay eggs but cannot start the garden. From the primitive *Cypomyrmex rimosus* to the specialized *Atta cephalotes* such females will gather sand grains together and manure them in a vain attempt to start the fungus growing.



The diameter of the tunnel that the female excavates is only slightly larger than her own thickness. She moves easily up and down in this as she excavates. The tunnel is 2 or 3 mm. in diameter in *Trachymyrmex septentrionalis*, 4 or 5 mm. in *Acromyrmex lundii* and 9–12 mm. diameter in *Atta cephalotes* and *sexdens* (Weber, unpubl.) (figs. 53, 54). It is also 9–12 mm. in *sexdens rubropilosa* (Autuori, 1942).

Soil from excavating the tunnel is scattered on all sides of the entrance in various *Atta* species. The female brings it up in the form of a pellet that appears to be agglutinated from her saliva. This pellet may be 5 mm. in diameter in *texana* (Moser, 1967) but smaller in other species that nest in clay instead of sand. The tunnel in *Atta* descends vertically to a depth of 15–25 cm. in *texana*. Where *sexdens* nested in sandy clay in Panama, the depths of three beginning colonies were 12, 19, and 26 cm., respectively. The same species in the white sand belt of Guyana in 1970 was found to have the initial queen's chamber in six cases at depths of 21 to 67 cm. (21, 22, 22, 27, 30 and 67 cm., respectively). Nests of *Atta colombica tonsipes* in red, wet clay in Panama were at depths of 7.5 to 12 cm.

The ant then enlarges the blind end of the tunnel at one side to create a chamber in which she ejects the contents of the infrabuccal pocket. Of 11 chambers in *Atta sexdens rubropilosa* in Brazil measured by Autuori (1942), the height

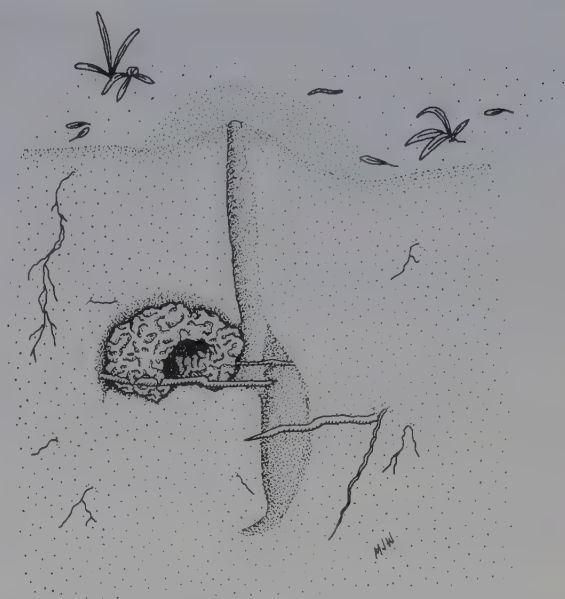


FIG. 54. The female of a young *Atta cephalotes* colony clinging to the side of her initial fungus garden. Her colony is about three months old. Orinoco Delta, Venezuela.

varied from 18–25 mm. and the basal diameters from 28 to 45 mm. Those of the Guyana nests above were similar. That of *texana* was about 50 mm., of the Panama *sexdens* above, 40 to 60 mm., and of *tonsipes* 35 to 70 mm. in diameters, probably reflecting slight differences in size of the chamber as a result of enlargement by a variable number of the first brood of workers.

#### CHANGES IN THE INTERNAL ANATOMY OF THE QUEEN

Eidmann (1935) described the female of *Atta sexdens* before the nuptial flight and much later when she was laying eggs. Before the nuptial flight the gaster was almost completely filled with greatly developed adipose tissue which enveloped all other organs. It consisted mostly of small, white, pearly bodies which lay loosely in the gastric cavity and which protruded when the integument was broken. They were considered to be single cells since in old queens the cellular nature was beyond doubt. The adipose cells in the young queen contained numerous vacuoles of different size filled with reserve material, distending the cells to capacity and compressing the protoplasm to a reticulum. The adipose body was the reservoir of the reserve material accumulated during the larval period,



FIG. 53. The female of a young *Atta sexdens* colony on her 33 mm. garden. This colony is less than two months old and the first broods had created a turret entrance to the nest. Panama.

which the mating female needed for the development of ovaries and the maintenance of her own metabolism during the foundation of a new colony. The sexual organs were still barely developed, especially the ovarioles and their hollow parts and ducts were not filled. The gut was empty and the malpighian vessels were white.

The adipose body virtually disappeared in the old queen; there were a few adipose cells or groups of them left between the organs. By far the greatest part of the abdomen was occupied by the greatly developed ovaries, which much predominated among the sex organs. The ovarioles formed two substantial clusters, among which all other abdominal organs were hidden. Study showed 258 ovarioles in one ovary. They were in coils and difficult to unravel. The length of a fresh ovariole was 7 cm. so that the total length of all of them in one old queen would measure 35 meters. The basal part of the ovarioles contained an average of 10–12 eggs with fully developed chorions and without nutritive cells making a total of 5,000 eggs ready to be laid.

#### FORAGING BY QUEEN ATTINES

The literature commonly carries the erroneous implication or statement that the new queen secludes herself while rearing her first brood and does not appear to the outside world. This is not true in various fungus-growers. The queens may open up the entrance to the nest and forage quickly for new substrate for her growing fungus garden. Conclusive proof is the presence of small sections of green leaves in a garden containing the first brood in the form of larvae and pupae. One of the clearest instances was in my lawn in suburban Buenos Aires where females of the common "hormiga negra" (*Acromyrmex lundii*) were seen to open their initial tunnels and dart out for substrate, then return quickly and fill the entrance from below with soil grains. The queen in a Trinidad *Atta cephalotes* nest had been bringing in fresh green-leaf sections. The behavior has also been observed in *Cyphomyrmex costatus* and *Trachymyrmex septentrionalis*.

The queen retains her versatility and this may enable a colony to survive, when, by some accident, many or all of her first brood perishes. In one case in *Trachymyrmex* (Weber, 1960) the queen and one worker survived in a laboratory colony but without any garden. When they

were then tested with small pieces of gardens of other species it was always the queen that reacted first and tasted them. Finally they were given a larger fragment of an acceptable garden, after I had first punched a hole in nearby wet sand with the eraser end of a pencil. The queen immediately went up to the mass and started to take it apart, moving it, piece by piece, to the prepared hole. She took the pieces part way down and plastered them to the inner wall to make a new garden. All the while the worker was accompanying her back and forth as a puppy dog without performing any useful work.

The females of all species are the most durable of all castes and generally are the last to die in a colony. In laboratory colonies of various small species it commonly happens that the workers and males die off early and a family of virgin females along with the original queen can maintain a garden successfully for a year or more. The virgin females usually lose their wings early, and for all intents and purposes act as workers.

#### RATE OF DEVELOPMENT OF YOUNG COLONIES

The queen lays eggs on the fungus garden as soon as it starts to grow.

The classical account is in *Atta sexdens* by Huber (1905). He in turn reviewed the pioneer observations of Sampaio (1894) and Goeldi (1904). Sampaio dug up an *Atta* female ten days after the mating flight and found a pile of 50–60 eggs. Three and one-half months later he dug out a nest which already had an open tunnel to the outside. There were about 150–170 small workers of variable sizes and eggs, larvae and pupae. Goeldi carried a colony up to the mature pupa stage and believed that broken eggs were used as substrate for the early fungus garden. On January 20, 1905, he started a series of studies on *Atta sexdens*; these studies were carried on by Huber. At the start there were 12 recently fecundated females and these were augmented by numerous females from flights occurring on February 23 and March 12. Huber described the appearance of 6–10 eggs after the third day and in his most successful case 40 days elapsed from egg-laying to first workers. In other cases as many as 63 days elapsed.

Bruch (1921) worked with *Acromyrmex lundii*. His excellent photographs of colony founding have been used by others (e.g., Forel, Goetsch, Wheeler).



He isolated 35 females that he considered fecundated since they had just lost their wings. These were taken after mating flights on October 18 and November 2, 1918. Ten were apparently sterile and soon died, one by one. Fifteen established, each separately, a fungus garden within 24 hours. Ten more did not develop gardens but lived a maximum of one month. Of the 15 females that formed gardens, one lived to the forty-fifth day, a time sufficient to complete larval development of her offspring.

Autuori (1942, 1956) used *Atta sexdens rubropilosa*. The nuptial flights and preparation of the initial nest of the females and then the emergence of the first workers were noted in five successive years. The average interval between the nuptial flight and the emergence of these workers was 87.2 days, varying from 72.0 days in 1938 to 93.9 days in 1937. The workers used the original opening first made by the female.

In my own study of *Acromyrmex lundii* in Buenos Aires in 1961 results were:

October 12—Five newly fertilized females placed together

December 23—Six callow workers not more than 1 or 2 days old observed

Temperatures were uncontrolled but were recorded as 16–24° C during the remainder of October, 17–24° C, in November and 20–26° C in December. The developmental period was thus about 70 days. Under warmer conditions, two months would undoubtedly suffice (see below).

Moser (1967) found *Atta texana* of Louisiana to rear the first brood some days before the fifty-eighth day from seclusion of the queen.

#### *The Queen as the Focus of Activity of Her Workers*

The central role of the queen in the activities of the young *Atta* colony is always shown by the constant attention that her offspring give her. She invariably has a number of minima to media workers walking over her and keeping her clean. In the laboratory one or more soldiers may take a position facing her and remain in this position for days (e.g., Weber 1945, Pl. 8 for *Atta cephalotes*). A young colony of *Atta sexdens* containing a single soldier of near-maximum size was transferred to a new observation nest with its dwindling garden whereupon the soldier took a stance facing the queen. The garden became still more reduced in size and the small colony

and garden were transferred to a new place again, the queen being picked up with clean forceps. Overnight her workers erected a small garden on her broad thorax and continued to care for both her and the garden until the two were again separated. The queen normally remains largely in one position on the young garden for many days at a time and moves slowly when she does move so that she does not damage it.

Ordinarily I do not risk handling young *Atta* queens for fear of rendering them unacceptable to their workers if they should release alarm pheromones, but I have on occasion. They have invariably been accepted back in the colony. The responses of the workers towards the queen as the center of their activities appear to overpower any alarm response.

#### COLONIES FOUNDED BY DIVISIONS OF LARGE COLONIES

It is possible that new colonies may arise by a splitting off from the parental nest in these generally placid ants. This does not necessarily involve a major separation. Recently fertilized females from a nuptial flight may descend near an existing colony, dig in nearby to initiate a new garden and then attract one or more randomly foraging workers from a neighboring colony. Success is most likely when the female comes from the same nest as the worker or workers. For example, a Guyana female of *Cyphomyrmex bigibbosus* was found with one worker in a tiny fungus garden. Two other workers were walking nearby. Since the workers were full size and unlike the dwarfs of first broods, it appeared that the female had adopted or tolerated them.

A stage in this type of split (Weber, 1941) may be represented by a series of gardens of the Panama *Apterostigma dentigerum*. A nest was found that consisted of four separate gardens in a horizontal crevice in the soil against a boulder. Workers wandered back and forth among all four. It seemed possible that a new queen could be adopted in one of the peripheral gardens.

In another colony of this species there were seven gardens over a distance of 115 cm. in a rotted log. Each contained workers and one or more alate females but only one queen which was of course dealate.

The foraging of the female of *Acromyrmex lundii* after forming her initial cell offers additional possibilities for adoption of workers if they should enter her young nest, attracted by



the odor trail of her pheromones, and adopt her garden. This is, however, not known. The queen and first brood of a Guyana *Atta sexdens* colony of 1970 was transferred to the laboratory in a dying condition, not being able to maintain the garden in transit. They were immediately adopted by workers with part of a healthy garden from a mature *sexdens* Guyana colony lacking a queen. Such cases are important to show how a mature colony whose queen has died may adopt a new colony or a single female on the periphery and thus maintain a nest site over many years through a succession of queens. A queen of *Acromyrmex octospinosus*, whose initial garden died, adopted a fragment of a garden with workers (Weber, 1967b); other queens foraged with workers (Cordero, 1963). The workers are attracted by the odor trail made by the queen of the species in all gardening ants.

The general evidence appears to be that 40 to 60 days may be average for rearing the worker. So far it has not been possible to mark and follow a particular egg so that the longer period may be due to all of the first few days' eggs being eaten.

Once the first workers mature, a new stage in the colony begins. They emerge to the outside, start enlarging the queen's original tunnel and the garden chamber, and bring in substrate. The subsequent stages are considered in chapter 6.

The queen at first had to assume the duties of the workers in caring for the brood and, for a time, raising the food. When the first workers mature, the queen is relieved of all functions except egg-laying (and conceivable caste regulation through pheromones). In the leaf-cutting ants of the two genera with the largest workers, first workers are relatively small. In one case in nature (Weber, 1967b) however, the first worker to mature was medium-sized and large enough to start leaf-cutting. In *Atta* the first worker duties are to care and feed the younger stages and tend the garden. A small size is advantageous for this. They can also drag pieces of substrate in to the garden but cannot cut green leaves.

Of seven Guyana colonies of *Atta sexdens* of 1970, four produced workers of 3–4 mm. length by the end of approximately  $2\frac{1}{4}$  months from queen fecundation, two produced 4–5 mm. workers and one colony had several of 5–6 mm. Two colonies in their sixth month had small soldier pupae and workers up to 8 mm. in length. Full-sized soldiers appeared the next month.

#### REPRODUCTIVE POTENTIAL OF THE QUEEN

Kerr (1961) produced strong evidence that the female of *Atta sexdens rubropilosa* is fertilized by several males and calculated the numbers of sperm in the spermatheca (the large, whitish bladder that receives the sperm and is ventral to the terminus of the gut in the female) and in the seminal vesicle of the male. Ants were taken from colonies on October 14, 1959, and October 18, 1960. To avoid the possibility that the females had been incompletely inseminated, he took females freshly descended from their nuptial flights that had lost their wings and were preparing to dig into the ground. To avoid examining the males that had released some of their sperm he chose those still at the entrance to the nest before leaving on the flight. Standard blood cell count techniques were used. Results in sperm counts were as follows:

Female	No. 1	— 319,125,000
"	" 2	— 206,500,000
"	" 3	— 262,600,000
"	" 4	— 226,270,000
Male	No. 1	— 44,126,000
"	" 2	— 80,134,000
"	" 3	— 56,000,000
"	" 4	— 58,800,000

The conclusion, therefore, was that each female could have been fertilized by from 3 to 8 males.

This evidence supports the inference that the queens in *Atta* may have an active egg-laying life of 10–20 years, during which the offspring of one could account for 2–5 million workers (only one queen is known in the Brazilian mature nest of *Atta sexdens*). The sperm that fertilize the eggs are maintained for all practical purposes as free-living cells, nourished and maintained in the queen's spermatheca.

Moser (1967) found that the full spermatheca of 16 queens of colonies 1–2 years old of *Atta texana* contained on the average 137 million sperm. Five females of older colonies contained 84 to 140 million sperm. Males contained on the average 100 million sperm in their seminal vesicles.

Poole (1970) concluded that the honeybee sperm was maintained in a low metabolic state as long as the spermathecal wall was intact. The factors in the maintenance of fertilizable sperm for the years of egg-laying in attines, however, have not been explained.

## 5. LIFE CYCLE OF THE ANTS

The life cycle of the gardening ants, like that of most other ants, comprises the stages of the egg, larva, prepupa, pupa, callow, and adult. Ants are derived from solitary wasps, most of which develop from egg to adult without parental care. The wasp's egg is laid in a favorable place, on the body of the prey in the usual predaceous or parasitic species, but is then abandoned. Social wasps make nests of cells. An egg is laid in each cell and the adult wasps feed the developing larvae at frequent intervals. Ants care for the brood continuously. Eggs are kept in a favorable place and moved about as the environment changes, especially with respect to humidity because of their inability to resist desiccation.

The fungus-growing ants differ from all other ants and all other insects, including the fungus-growing termites, in embedding their brood in the fungus garden, where they are normally covered by the thread-like mycelium. In the one yeast culturer (*Cyphomyrmex rimosus*) the fungus covers the brood in a mycelial form, although the same fungus when cultured for food on insect excrement occurs in the form of masses of yeast cells. The attines carry their brood about and it facilitates their handling of a mass of eggs to have them embedded in a mycelium. The average species will have all stages of the life cycle present in the nest at one time. As already noted, the soldier form of the *Atta* worker ordinarily is produced after the first seven months of colony life.

### THE BROOD

#### EGGS

Eggs of attines are elliptical and white (fig. 55). They are ordinarily difficult to see in the fungus garden because of the coating of hyphae that normally covers them. After the female has laid the eggs they are usually taken to a nearby cell and embedded in a wall. Commonly they are in clusters of variable numbers and these may have a general mycelial covering. The eggs of the castes seem all alike.

When observation nests with eggs are placed on the stage of the microscope for study, the ants regularly respond by moving them out of

the light. This corresponds to behavior when nests are broken open by natural invaders.

The size of the egg is not correlated with the size of the ant. The occasional egg found in the minima worker of *Atta cephalotes* is comparable in size to that of the queen weighing some 800 times more. A common egg size in species of five genera including *Atta* is  $0.45 \times 0.32$  mm.

Bazire-Benazet (1957) examined the development of the egg of *Atta sexdens rubropilosa*. She followed Autuori in naming the small eggs as the reproductive type, the large eggs as the alimentary or nutritive. If by chance the latter are not eaten they become covered with hyphae in the garden and do not develop.

She found that the two types of eggs can be produced by the same ovariole. It is not rare to find a reproductive egg ready to pass into the calyx at the base of an ovariole, immediately followed by an alimentary egg, equally mature for laying. The formation of the alimentary egg may be seen in the distal or end filament. Bazire-Benazet figured an alimentary egg in the process of accumulating its reserves, in broad connections with its nutritive cells which send extensions into the nutritive chamber of the egg preceding them. The degenerated condition of the nutritive cells showed that they have nearly completed their contributions. Some contribution cannot be excluded from the follicular cells as the egg passes by them.

Both types of eggs become enclosed in the same follicle wall, which appears to be the result of separate walls fusing. The membrane separating the two eggs in the follicle subsequently breaks and disappears. She was not sure whether or not two eggs participate in the formation of one alimentary egg. It is not known what the ratio of the two types is but the alimentary type is characteristic only of the early colony stage.

#### *Eggs Laid by Workers or Virgin Females*

Unfertilized eggs in the gardening ants are known only to be eaten or to develop into males. Isolated virgin females of *Acromyrmex octospinosus* laid a few eggs from time to time and three larvae developed three months later in one record but did not survive. These would have

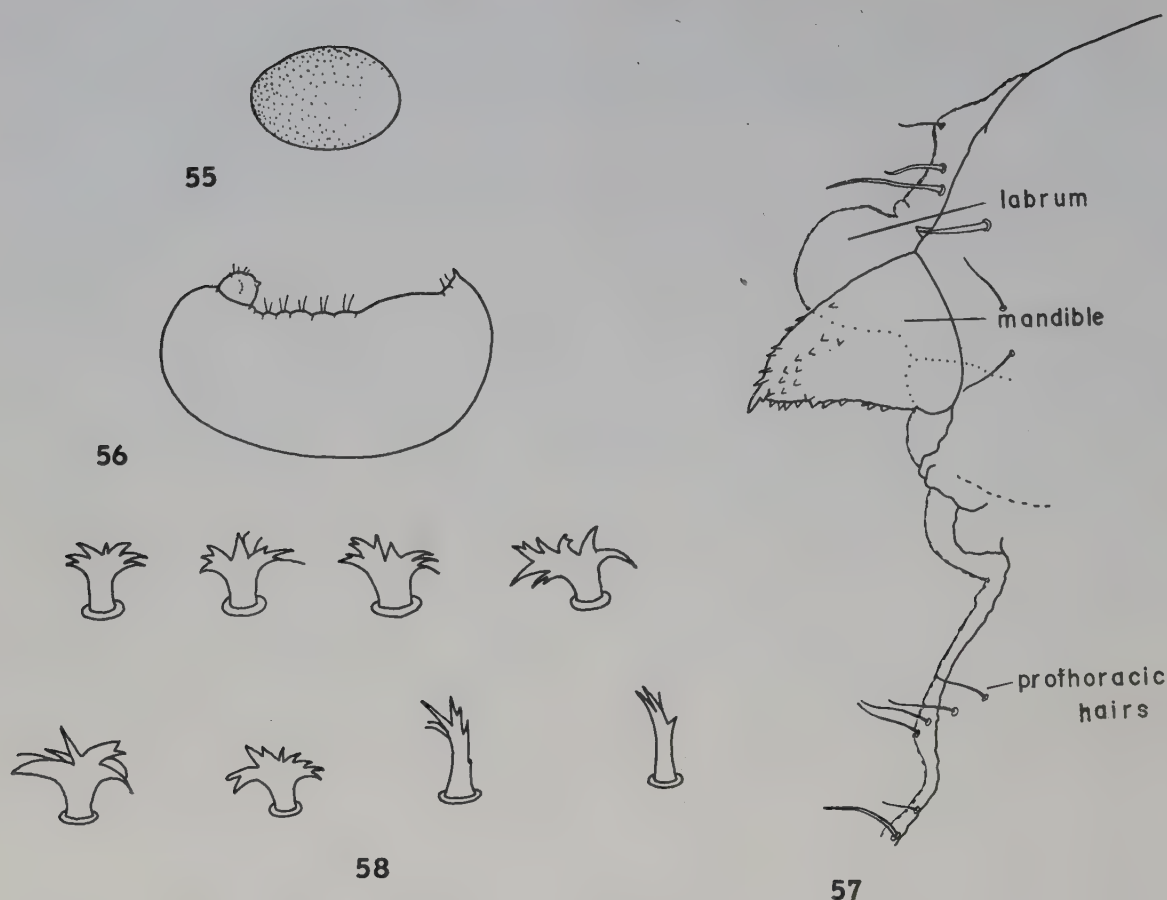


FIG. 55. An egg of *Cyphomyrmex rimosus* from a Florida colony. It was 0.17 by 0.24 mm.

FIG. 56. A larva of *Trachymyrmex septentrionalis* showing the ventral hairs common to many larvae. The head capsule is to the left, the anal hillock to the right. New Jersey.

FIG. 57. The head capsule of the larva of *Trachymyrmex diversus* from the side, showing the spines on the mandible that are used for puncturing the filaments of fungi. The thoracic hairs help to hold the fungus. Guyana.

FIG. 58. Hairs of the larva of *Acromyrmex octospinosus* that cover the body sparsely and are used for holding the larva in the fungus garden. Such hairs are not common to most attines and these show a diversity in form. Venezuela.

developed into males in all probability. Isolated minima and maxima workers of *A. lobicornis* performed similarly, the eggs maturing as far as the larval stage within two months of isolation. Dissection of minima and small media workers of *Atta cephalotes* showed single but full-size eggs in a few of them. They would probably have been eaten if laid.

#### *Duration of the Egg Stage*

The length of the egg stage is not clearly known in most cases because it is not usually sure that an egg that is noted on one day is the same as one that goes on to develop. It may have been eaten and replaced by another on a subsequent date. However, in *Atta insularis*

the duration is reported as 15–16 days (Bruner and Barry, 1949) and in *A. sexdens rubropilosa* 22 days (Autuori, 1942).

#### LARVAE

As development within the egg proceeds, the embryo shrinks somewhat from the chorion. The larva leaves through a hole gnawed in the side. The mandibles of the larva are spiny (fig. 56) and rasp the hole as the larva opens and closes its mouthparts, thrusting the head capsule up and down in the meanwhile. These may be reflexes of a hungry larva.

The larva is legless and eyeless as in ants generally. There are 3 thoracic and 10 abdominal segments. Of the 10 stigmata, 2 occur



on the thorax. Full descriptions of larvae are given by G. C. Wheeler (1948).

Details of the hatching of the larva are difficult to observe when the event takes place in a mass of slightly younger eggs within the usual mycelial coating. The change from the egg to the larva is, however, clear since segmentation of the larva and the dark gut are easily seen through the semi-transparent skin.

In a *Trachymyrmex septentrionalis* experiment, several isolated eggs hatched and the ventral surfaces of the new larvae were immediately applied, apparently by their own rotation, to the mass of eggs and mycelium. In one case the anal end was free while the mouthparts were embedded in the mass. On the day of hatching the dark gut was visible. Mouthparts were observed to be working and feeding on the discarded chorion or the mycelium. One larva doubled its bulk in two days.

Larvae of some non-attine ants are fed solid food and have limited powers of locomotion, wriggling to or in an insect carcass brought by the adults. They are later placed in favorable sites for spinning the cocoon or pupation.

Larvae of the gardening ants differ in their lack of locomotion and absence of the cocoon. They are frequently licked by the adults. Saliva is thus added to the integument and apparently this enables the fungus to grow freely over it. The fungus usually grows into the garden so that to some extent the brood is a part of the substrate of the garden. The fungus covers the early broods of all species although it may be largely absent in older *Atta* broods. The larvae must take in enough food to carry the ant through the pupal stage to the adult. They have to be fed and in theory they might be able to feed themselves if embedded in the fungus. They do not appear to do this to any appreciable extent and only when very small. Mouthparts of larger larvae are usually out of range of the fungus.

Larger larvae are usually embedded in the garden with the head capsule protruding. It does not matter whether the larva is on a side or on its back as long as the mouthparts are free. By "pouting," or extruding the mouthparts, it notifies workers of its hungry state and they respond by placing a mass of fungus on them. When the workers lick the larval skin they may derive substances which are, at least, attractive and may be of great significance.

This trophallaxis, or mutual feeding, varies

according to the animal. The special role in the larva of the wasp, *Vespa orientalis*, has been described by Ishay and Ikan (1968). Colonies cannot exist without the larvae, whose salivary secretions are the only source of raw material for nitrogen metabolism and egg production available to the workers and the queen. The latter members of the colony do not possess the proteases necessary for protein degradation. Such studies have not been performed with attines but it is clear that larvae are an integral bond in keeping a colony viable in addition to keeping the generations going. The constant licking that their integument receives may be both a source of nutrition for them from the worker saliva and larvae may give off exudates which are in turn imbibed by the worker. In any case, the substances that are passed, including possibly pheromones, help to unify the colony. A nest without larvae and the queen comes to an end within a year. The workers become sluggish and cut little or no substrate after a matter of days or several weeks. The mycelium soon deteriorates, creating less and less food for the survivors. This vicious cycle will begin shortly after the queen dies or is removed. Her own pheromones, picked up and distributed by the nursemaids, must be the original unifying factor in a colony.

Ant larvae in general are covered with hairs, which may be diverse in form but serve to keep the integument off the moist earth or to prevent too close contact of individuals with one another in the usual situation. This is true of such myrmicine ants as *Pogonomyrmex* and *Myrmica*. Another function of the hairs is to serve as anchors to the walls of the nest chamber. They are commonly sinuous in form, giving resiliency to the larva as it is moved from site to site by the worker.

The larvae of gardening ants, however, have a special need for ventral hairs (fig. 56-57) to hold the fungus, on which they are feeding, firmly in place. They generally lack hairs on the sides and dorsal surfaces of the body with a few spectacular exceptions (e.g., *Acromyrmex*) so that, except for the head and ventral area much of the integument is naked. The hairs may be confined to the ventral surface of the head, thoracic and anal regions. The body hairs of *Acromyrmex octospinosus* are particularly stout and multifid (fig. 58), but being borne on tubercles in *A. lundii*. The sparse hairs of *Cyphomyrmex rimosus* may be finely divided

apically. Larvae of this species are unique among ants in their need to hold a bromatium, which is a compact mass of yeast cells, but the hairs are not especially adapted for this purpose and the fungus is held more by the spinulose mandibles. All larvae handle a mass of fungus effectively with the mouthparts and use the ventral thoracic body hairs mainly for keeping the fungus within reach. The anal hairs hold an anal droplet from time to time which the workers may remove.

#### *Feeding of Larvae*

Although the fungus cultured by *Cyphomyrmex rimosus* is a yeast, the details of larval feeding of this ant are essentially as in the attines which culture a filamentous form of fungus (Weber, 1955).

The compact masses of yeast cells (bromatia) are placed directly on the mouthparts of the larvae. A worker may remove the partially eaten mass from one larva after a minute or two and give it to another larva. Or the first larva may entirely consume the bromatium. It will then work its mouthparts in and out for a moment and move the entire head capsule up and down slightly. The nursemaids regularly feel the larval mouthparts with their antennal apices and may also lick them.

The feeding of the larvae is remarkably similar in all attine species. Most of the species culture clusters of inflated hyphae (staphylae) and the use of this compact form of the fungus is particularly efficient. The ants, however, feed upon the ordinary hyphal strands as well, and this is all that is available in *Apterostigma*. Feeding whole staphylae or bromatia is reminiscent of the more primitive type of feeding, as in Ponerinae, where whole pieces of insects are placed at the larval mouthparts. Myrmicines such as *Pheidole* may also use this method. Regurgitation of liquid food from the worker would appear to be possible always but would seem more useful in the smallest larvae.

Attine larvae may feed for minutes at a time on a hyphal cluster. The larval mandibles grasp the food easily with their sharp apical teeth and denticle-covered surface (fig. 57). The labrum or upper lip is a thick spinulose flap, the maxillae are long and narrow and the labium or lower lip is small and short. It appears that the spines and pressure on the fungus by the mandibles alone would be sufficient to break the fungus walls.

#### *Artificial Feeding of the Larvae*

Larvae of *Trachymyrmex septentrionalis* two millimeters long were isolated experimentally on damp quartz sand and directly fed with hyphal clusters. The well-formed, compact and roughly spherical masses of hyphal inflations were about  $\frac{1}{4}$  mm. in diameter. These were picked up on the point of a No. 00 insect pin that had been inserted in a match stick. The mass was then transferred to the vicinity of the mandibles and stuck to the hairs posterior to the mouthparts. The larva then proceeded to feed on it. Or the larva would feed directly on the fungus stuck to the pin point and would consume it completely. In one case a larva, freshly removed from the ant nest, ate seven clusters, one directly after another. Among the possibilities of such experimentation are the feeding of larvae with fungus from another species of ant and the feeding of radioactive or dye-marked fungus to determine possible transfer of materials between larva and adult such as by licking.

In nature larvae may be fed not only fungus but also the ant eggs. The eggs of the above species have a tough chorion not easily punctured by the larval mandibles, since the eggs are hard to grasp firmly. However, when an egg was experimentally placed over the mandibles and punctured with a fine insect pin, the larva immediately ingested the liquid contents.

Larvae also ingest other liquids. When a neutral dye, such as Nigrosin, is ingested, the course of its passage in the gut may be seen dimly. The fore gut itself shows as an elongate tube taking up most of the length of the larva. Dorsal to that is the heart and blood vessel, the former pulsing slightly. Lateral to the mid-dorsal structures appear the milky islands of fat cells which obscure deeper organs.

A special case of larval feeding was witnessed in a 1970 nest of a queen of *Acromyrmex octospinosus* that was rearing her first brood with the aid of a minima worker and garden fragment introduced from another colony. The brood consisted of eggs and several larvae, of which one was of medium size. This was fed a much younger larva that had been placed on its mouthparts and it spent fully a day gradually ingesting the contents of the smaller larva.

#### PREPUPA AND THE PUPA

The larva passes into the prepupal stage. The very small head sits like a small appendix on the



humped, distended prothorax. This latter contains the powerful pupal head which causes the distention. The skin is tightly stretched and the abdominal segmentation is scarcely recognizable. Hairs are sparse, short and limited to the head, prothorax, and last abdominal segment. The larval skin may be left at the anal end.

The pupa is naked and striking in the strong sculpturing of the head, especially on the frons, which in several genera is covered with numerous protuberances as well as with both occipital spines that the adult of most species possesses. The pupa is snow white at first; color begins to show at the eyes and masticatory margin of the mandibles. The sutures then become delimited. The development of pigmentation furnishes a useful chronology as worked out in *Trachymyrmex septentrionalis* (Weber, 1966) (fig. 59).

*Pigmentation of the Pupae of Trachymyrmex Septentrionalis*

Pigmentation arises first in the compound eyes of all castes. These acquire a faint brownish color which gradually deepens to almost black before pigmentation appears in the rest of the body. Ocelli of the males and females acquire pigmentation also before the rest of the body. The skin of all castes acquires a faint brownish tinge next and this gradually deepens to a dilute brown. The wings of the female become dark brown while the skin is much paler.

Male pupae, kept at 22–24° C, can first be recognized when they are at the characteristic white, unpigmented-eye stage. Thirteen days later they are pale brown (fig. 60) and four days afterward they can move the terminal gastric segments and other parts of the body.

The pigmentation of the eyes and ocelli in the female pupae is followed by a faint brown rim to the mandibles, indicating the masticatory margin, followed by a brownish outline to some of the thoracic sutures. At this time the pupa is a dirty white. As it becomes a pale brown the mandibular margins darken, the frontal ridges become brown and all tubercles become faintly indicated. The wing pads darken distally before they darken proximally. The mandibles may be moved while the body is still a pale brown.

Worker pupae follow a similar pattern with the masticatory margins of the mandibles darkening after the eyes have become dark.



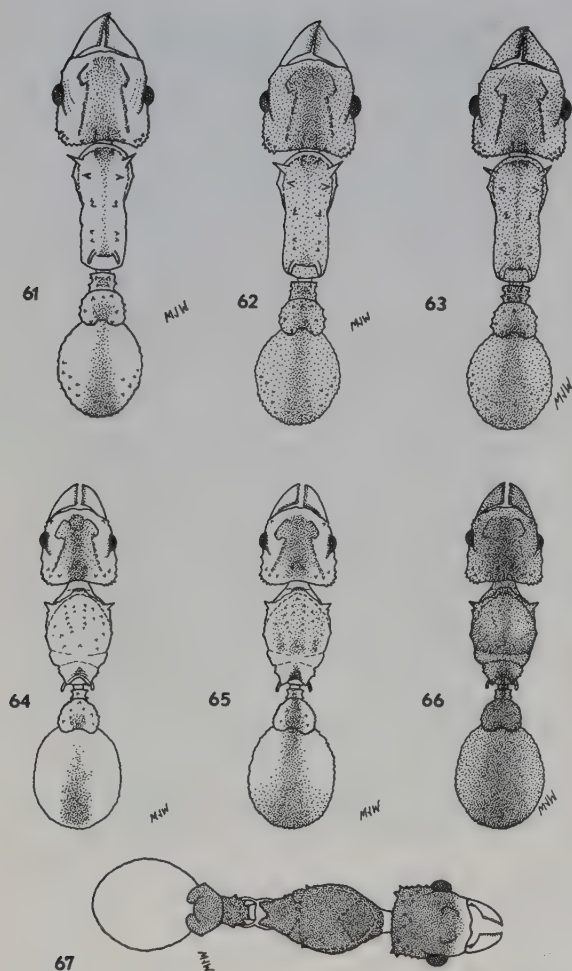
FIG. 59. Soldier pupa of *Atta cephalotes* at an early stage when the eyes have become pigmented from their original white. Trinidad.

Female pupae can be recognized as early as the males, the females show the wing pads at the sides of the body between the first and second



FIG. 60. Male pupa of *Trachymyrmex septentrionalis* in side view at the beginning of pigmentation. The wing pads are between the second and third pair of legs. The ant is covered tightly with a thin pupal envelope (exuvia) that will have to be licked away by workers before it can become an adult. Otherwise it will die since it cannot emerge from the exuvia without assistance. New Jersey.





FIGS. 61-67. The castes of *Trachymyrmex septentrionalis*, from above, with appendages removed and showing the development of pigmentation from the callow to the adult in three weeks. (61) worker, 1st week; (62) worker, 2d week; (63) worker, nearly adult pigmentation; (64) female, 1st week; (65) female, 2d week; (66) female, nearly adult pigmentation; (67) male, 1st week.

pairs of legs as in the male. Both show the characteristic configuration of the head of the sexual castes. The female head is also much larger than that of the worker and soon shows the ocelli which they lack.

At 22-24°C the duration of the pupal stage of both males and females was eighteen days.

Isolated pupae could mature from beginning to end of this stage but could not emerge unassisted to the callow adult state in one experiment. They acquired mobility of the head, mouthparts, fore legs, and trunk but could not release all legs because of the tight pupal en-

velop without assistance from workers (see beyond).

#### ADULTS

Adult ants of all castes emerge from the pupal state as callows. These are characteristically pale at first and walk unsteadily. They are full sized and now start feeding independently on the fungus.

#### CALLOW

The emergence from the pupal to the callow state takes several hours and much attention from the attendant workers.

A female of *Trachymyrmex septentrionalis*, for example, was assisted initially by five workers as she became a callow. Her wings were a dirty white, not showing any of the black characteristic of the pupal state. The four wings were being bent and handled separately by the workers as they were licked. Every part of the integument, including all exposed appendages, was being licked by the five adults. The female was standing, in the meanwhile, on the fungus garden on pale yellowish legs, which by now were of normal dimensions as contrasted with the inflated size while pupal. The brown pigmentation was confined to the dorsal areas. The head was brown. The scutum (dorsal plate) of the thorax had three dark longitudinal streaks and the gaster had one.

At times there would be two workers on each side of her head, two on the thorax and one or two at the gaster, six workers being the usual maximum for which there was room although seven were seen once, all licking the integument. The hind wings could be rotated separately as much as 200-300° without apparent harm and the fore wings were rotated fully 200°.

This continuous and intensive licking may condition the new-born at a critical time in its life history to development of a behavior pattern of importance to social insects and to fungus-growing ants particularly. The colony odor also must be transmitted then to the new-born.

All castes remain in the cells of the garden the first day or two. Pigmentation of the female and worker in *Trachymyrmex septentrionalis* proceeds as follows: (a) mid-dorsal longitudinal streaks become darker brown on the gasters; brown blotches appear on the nodes dorsally; (b) brown thoracic streaks in the female become darker and the body in the worker darkens generally; (c) the general body color becomes a

dark ferruginous and the above dorsal streaks become less conspicuous (figs. 61–67).

Males are able to walk about in the callow condition while much paler than mature adults. The wings at first appear milky, then a dead gray to black. The dorsal surface of the head also is nearly black although the ventral surface is brown. The gaster and legs are pale brown while the thorax is variably darker brown.

#### ADULT WORKERS

The minima in *Atta cephalotes* play an important role in development. It is they particularly that swarm over the maturing pupa, licking and tearing the pupal envelope until the callow emerges. Eight or more minima may be on one large worker or soldier at one time. Some will be licking the pupal skin, others pulling at it with their sharp mandibles and shredding it. They appear to ingest such particles, probably to lodge in the infrabuccal pocket and later be regurgitated. The mouthparts of the minima are extended to their fullest, the hypopharynx or tongue being fully inflated. This has a series of fine, sharp spines that form an effective rasp.

The soldier, once released from its pupal envelop, is honey brown in color, with its inflated occipital region appearing laterally smooth and shiny. The silky pubescence of the frons is free as are the hairs elsewhere on the body and the short spines of the tarsi. The nursemaids, which may include more than the smallest ones, continue to lick all parts of the body, including the largely extended mouthparts. The palpi here are also free and extended. The mandibles at this stage are a moderate brown in color, much paler than the dark brown of the adult. The eyes, with facets clean and shining, are black and contrast sharply with the body. The soldier may be resting passively on its side, motionless although capable of moving its appendages and being tugged at from different sides by the workers. It darkens gradually in a week or two to the permanent adult brown color. This adult color is much darker, dark red brown to almost black, in other species.

#### Grooming

One of the activities of peculiar importance in the gardening ants is grooming or care of the integument, whether by the ant of its own integument or as assistant to other members of

the colony. The details of grooming appear to be similar among all species.

In grooming itself, an ant uses the strigil at the end of the tibia of each fore leg, drawing the legs of the opposite side between it and the curved, adjacent first tarsal segment. The near surface of the latter bears a row of dense, short bristles. The terminal segments of the antennae are kept constantly cleaned in the same manner. Detritus from this cleaning tends to collect in the infrabuccal pocket off the pharynx. The body is scraped with the short dense bristles of the ventral surfaces of all tarsal segments and the total effect is to keep the ant extremely clean. The ants spend much time cleaning one another. The one being cleaned remains passive while one or more members of the colony go over it thoroughly with their mouthparts (fig. 7, 11). The mandibles may be opened or closed and are not used. The tongue of the groomer is appressed to the integument and is applied thoroughly to irregular crevices as well as to flat surfaces. It is in the form of a minutely ridged swab that is moist with salivary secretions.

The *Atta* queen is so bulky and large as to be incapable of cleaning all parts of her own integument. The smallest workers go down into her narrowest crevices, such as between the head and the thorax, and lick them carefully (fig. 9).

Foraging ants come into contact with a host of organisms such as alien fungi, bacteria, protozoa, and parasites which would be harmful if taken into the nest. Grooming must play a significant part in inactivating those on the integument that might proliferate in the constantly humid air in and about the garden.

#### *Appearance of the worker sizes in Acromyrmex and Atta*

The minima worker in both *Acromyrmex* and *Atta* is usually the first to appear in young colonies, although the first pupa to develop in one nest of *Acromyrmex octospinosus* in nature matured as a media (Weber, 1967). Among the first 50–100 maturing *Atta cephalotes* and *sexdens* workers in nature in 60–70 day-old colonies were small media (4–5 mm.). By the end of the fourth month, in the laboratory colonies of *cephalotes* at 26–27° C, 6 mm. media workers were in evidence and in the sixth month maxima workers to 8–9 mm. appeared. Laboratory colonies of *Atta sexdens* from Panama kept under similar conditions contained workers up to the 8–9 mm. size by the ninth month and those of



*Atta colombica tonsipes* had developed the same sizes by the seventh month. Autuori (1941) found workers from minima up to but not including the soldier size in *Atta sexdens rubropilosa* in the fourth to tenth month of colony life.

Soldiers in *Atta* are the last of the worker caste to appear. Autuori (1941) found them appearing 22 months after colony founding in *Atta sexdens rubropilosa*. The first soldier of *Atta cephalotes* to appear outside a nest of known age in Trinidad came in the eleventh month and in sister colonies kept in the laboratory at 26–27° C a 11 mm. soldier matured after 4½ months of colony life. Other soldiers in the colonies matured after 5–7 months.

Soldiers of 10–11 mm. length matured in laboratory colonies of *Atta sexdens* from Panama in the ninth month (seventh month in Guyana colonies) and in similar *Atta colombica tonsipes* colonies 10 mm. soldiers matured in the seventh month.

Three colonies of *Acromyrmex octospinosus* that originated from females fertilized in nature on July 1 and were kept at 25–27° C in the laboratory matured about 50 minima and media workers in each of two colonies by March 7. Some 200 were then present in the third colony. By March 14 the latter colony produced the maxima worker size.

When the colonies were a year old in 1966 they had worker populations of some 150 (68 medias counted), 200 (120 medias counted) and 800 (300 medias counted). A second colony had the maxima workers by August, 1966. Two of the colonies had female broods in March, 1967, and April, 1968, respectively.

#### LENGTH OF LIFE CYCLE

The length of the life cycle from egg to adult depends in part on the species of ant and in part on the temperature; the higher the temperature the faster the development. The following are representative laboratory records and pertain to the worker caste unless otherwise specified:

The minimum developmental period known was one month at abnormally high temperatures of 26.4–33.5° C in a colony of *Trachymyrmex septentrionalis*. The first to mature was a male, followed by other males and females and workers. Other colonies of this species were like those of *Cyphomyrmex costatus* and other species in taking approximately two months at 21–25° C for the three castes. The larval period was about one month in several colonies of these and *Myceto-*

*phylax conformis* but the combined egg and larval period was one month in a *septentrionalis* colony. It was 6½ weeks minimum for the egg to adult period at 24–25° C in a *Mycetophylax conformis* colony.

The developmental period for *Acromyrmex lundii* in Argentina was approximately 2½ months at temperatures that started with 16° at the beginning and terminated at approximately 24° C. It was 63 days minimum for *Acromyrmex octospinosus*; of which the egg stage took 24 days, the larva 18, the semi-pupa 5 and the pupa 16 days at 25–26° C.

Autuori (1942, 1956) determined this time for brood stages for *Atta sexdens rubropilosa* in Brazil by digging up numerous colonies of females after known dates of insemination. These periods were 5 days pre-ovoposition, 22 days for the egg, 22 days for the larva and 10 days for the pupa. He also found that the first workers may stay underground about 20 days before they tunnel out to the soil surface.

Bruner and Barry (1949) reported that the brood times for the Cuban *Atta insularis* was 15–16 days for the egg, 9–22 (average 17) days for the larva and 11–15 (average 14) days for the pupa.

#### LONGEVITY

The males are the shortest-lived caste, living usually only 1 to 4 months, and the functional female or queen of the colony is by far the longest lived. Anatomical evidence indicates that the female has an enormous reproductive potential that might take years to realize (chapter 4). A female of *Myrmicocrypta buen-zlii* lived more than 5 years in the laboratory. The female of a captive *Trachymyrmex zeteki* colony lived more than 5 years (Weber 1964) and one of *T. septentrionalis* lived 7 years and 4 months. Urich (1923) alluded briefly to a female of *Acromyrmex octospinosus* in a 7-year colony and I have kept one for more than 8 years in a thriving colony. One would expect the *Atta* queen to live 5–10 years (one of my *cephalotes* is over 7 years old) and, one of *sexdens rubropilosa* in São Paulo, Brazil lived 22 years (Amante, 1970, pers. commun.)

Workers, active as they are throughout the day, might be expected to be as short-lived as those of the honey bee but this is not the case in laboratory colonies. Workers of *Trachymyrmex septentrionalis* were known to live at least 19 months (Weber, 1956a) and later workers lived



more than 2 years. The situation in nature may well be comparable so far as total life span is concerned. These captive ants were active many more months than those in nature in New Jersey. Here the larger number of workers may well die during the fall and winter after an adult life of only one season (some 5 months) but some will survive to a second season. Other evidence as in *Myrmicocrypta buenzlii*, *Trachymyrmex zeteki*, *Sericomyrmex urichi* and several *Atta* species indicates a worker life of 1 to 2 years. The first workers of several new *Atta sexdens* colonies of Guyana lived 6 to 9 months.

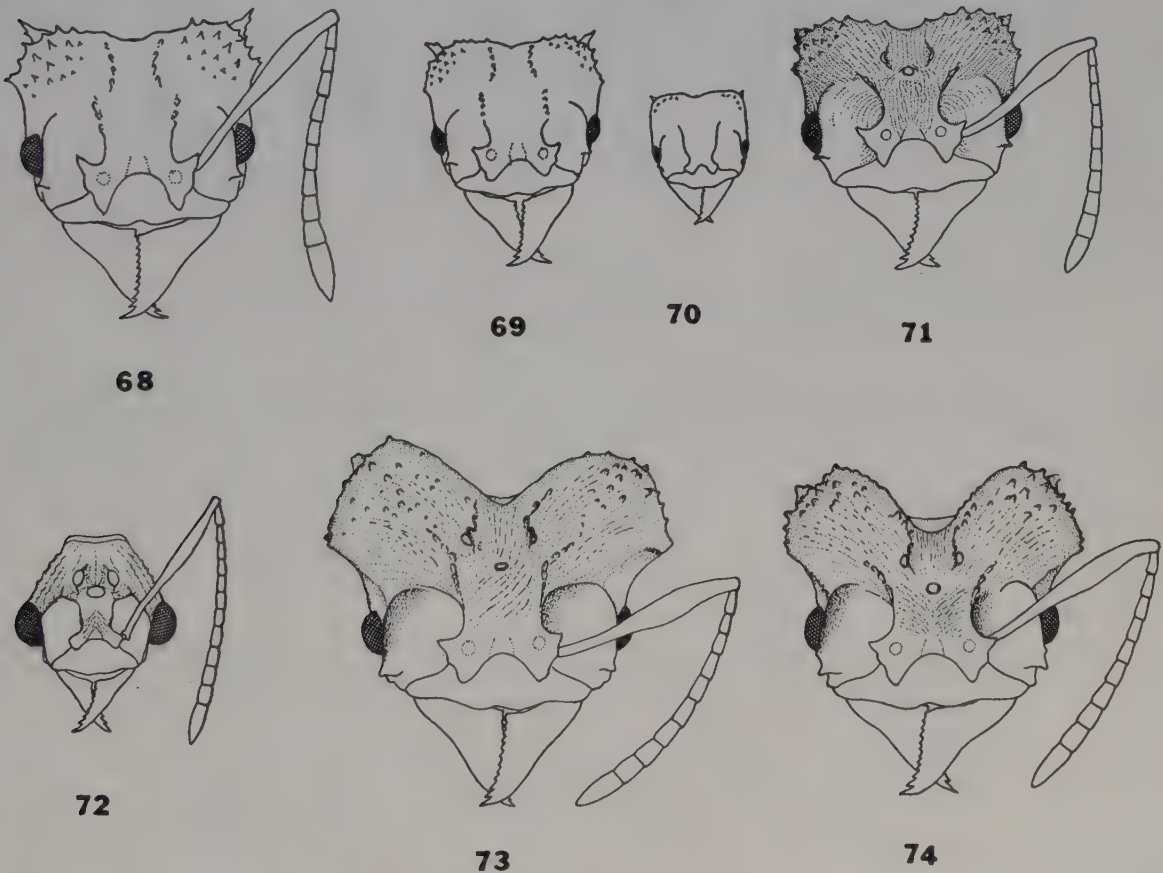
#### DEVELOPMENTAL ANOMALIES

Minor freaks or anomalies are not unusual among single individuals of all animals, but when an entire colony of a social animal shows a condition of this type in nature, it is most unusual. The following record is tantalizing and badly needs an explanation.

Two colonies with unprecedented numbers of anomalous ants were taken by me in 1934-1935 in Trinidad, West Indies. One consisted of the non-attine, *Cephalotes atratus*. The second colony was that of the fungus-grower, *Acromyrmex octospinosus* Reich (fig. 68-76). These were characterized by Wheeler (1937) as gynandromorphs and by Whiting (1938) as intersexes.

This colony contained 8,012 normal-appearing individuals, including 11 dealated females. Erroneously, the latter were assumed by Wheeler to have been mated, but it is not unusual for old virgin females to lose their wings and it is possible that a single fertilized female was the mother of all of the anomalous ants. There were 660 alate males, 175 alate females, and 7,166 workers. The latter were grouped as 56.2 per cent minima, 30.2 per cent media, and 13.5 per cent maxima.

There were 163 anomalies, including (by Wheeler's terminology): 6 mutant females, 101



FIGS. 68-74. The castes and anomalies of my *Acromyrmex octospinosus* Trinidad colony after Wheeler, 1937. (68) head of the worker caste, maxima; (69) head of the worker caste, media; (70) head of the worker caste minima; (71) head of the female; (72) head of the male; (73-74) two scrobiculate anomalies.

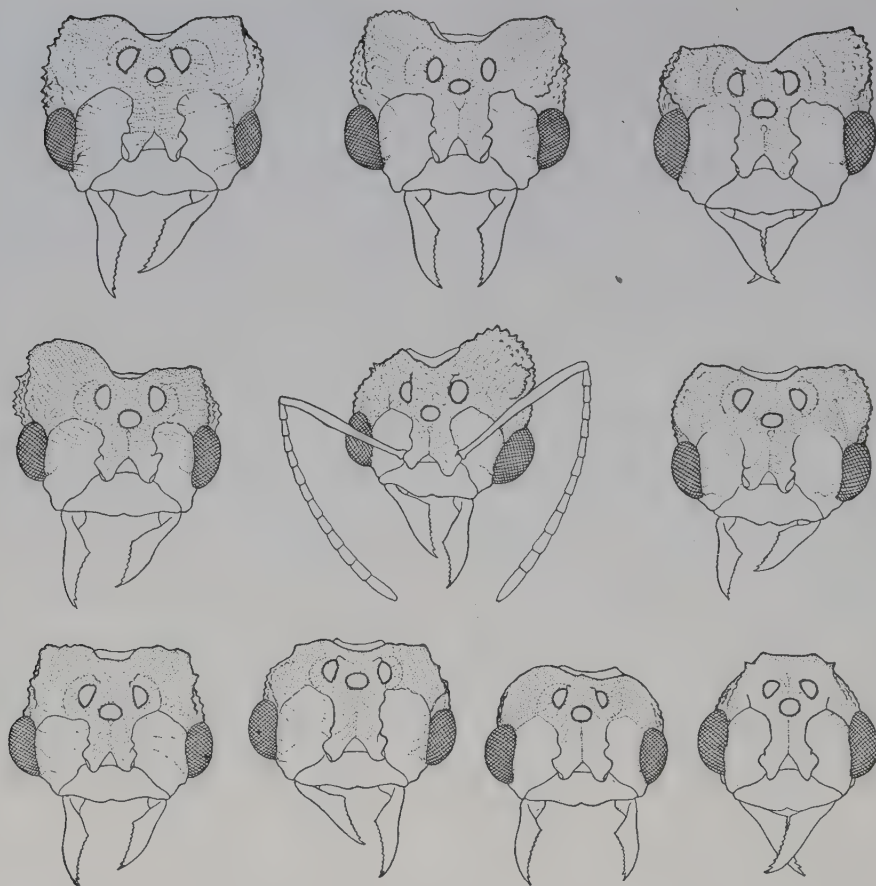


FIG. 75. A series of male-female intersexes; the larger side of the head reflects the female tissue; both sexes have ocelli but the male has larger compound eyes.

mutant workers, 46 gynergates (female-worker combinations), 1 diploergate (minima-media worker) and 10 gynandromorphs (female-male combinations).

A single dealate female was unusually rugose and dark. Wheeler speculated that she might be the mother of 100 maxima and media workers which were much darker and rougher than the other workers. Whiting considered these 100 to be intercastes.

A pale, spotted type was represented by one dealate and two alate females and a single large worker.

A scrobiculate type was represented by one dealate female and a winged female, both of small size (figs. 73, 74). They had anomalous heads with 12 separate peculiarities, the 2 most conspicuous being the cordate head and arcuate ridges or carinae which close the frontal scrobes posteriorly as in males. Whiting considered

these to be female inter sexes. He suggested the possibility that they may have started life as maxima workers, then shifted early to females and still later to males because of the complete frontal scrobes. The dealate female was regarded by Wheeler as the mother of 10 gynandromorphs (male-female mosaics), 46 gynergates (female-worker mosaics), and the single diploergate (maxima-media worker).

The female component in the 10 gynandromorphs was confined to the posterior part of the head except that in one there was feminization of the genitalia. The heads formed a series ranging from very broad as in the female to narrow, approaching the male. The antennae were of the 13-segmented male type and the wings were perfectly developed in all except one, which was dealate. Whiting suggested that these 10 were male intersexes of differing grades, showing feminization in more or less superficial traits.

He suggested further that the asymmetry is to be expected for it is characteristic of many aberrant types. "In some cases, as in triploid intersexes, it involves genetic mosaicism brought about by chromosome elimination. More frequently, however, it is due merely to a delicately shifting physiological balance."

All 46 gynergates had bodies indistinguishable from those of maxima or, more rarely, media workers, but the head was in every case dark brown or blackish as in the female. The antennae were of the usual 11-segmented worker or female type. The series could be roughly divided into three groups which showed transitions from more or less symmetrical antero-posterior to very asymmetrical right- and left-

segregation of the worker and female characters. None showed any trace of ocelli that the female and male possess. Whiting interpreted these as worker inter castes which began development as workers with a turning point too late to involve production of ocelli. The closure of the scrobal arches, which occurred in the great majority of these anomalies, was a trait of relatively late developmental determination according to Whiting. The fact that these arches were closed in the male indicates that these intercastes were also intersexes. The 5 specimens that had open scrobes may represent regressive fluctuation toward the normal maxima worker.

The single diploergate had the body of a large media worker, but the left side of the head

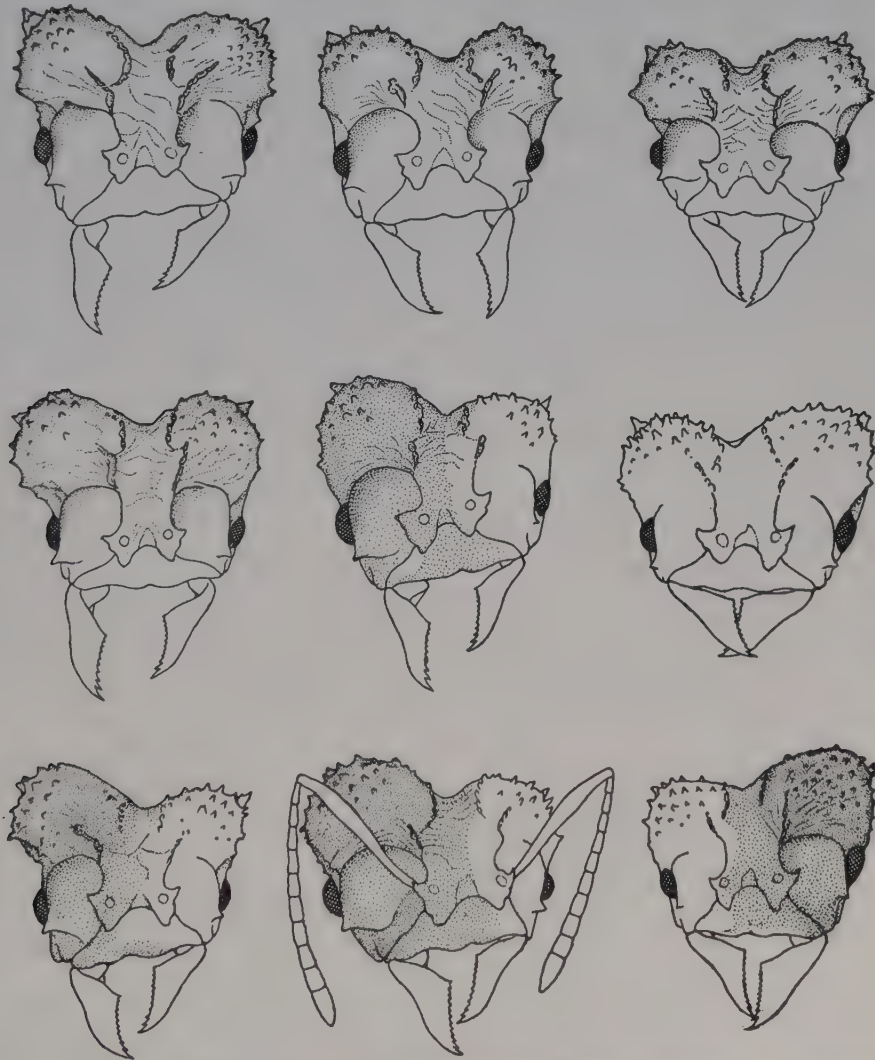


FIG. 76. A series of anomalies interpreted by Wheeler as female-worker mixtures; note the asymmetries.



was enlarged, resembling that of a maxima. Whiting considered this a media worker intercaste with a late turning point toward the major.

He believed that the reason for the abundance of anomalies in both the *Acromyrmex* and the *Cephalotes* colonies is undoubtedly genetic. "It may be supposed that race mixture is here involved (strong with weak as in Goldschmidt's *Lymantria*) and that different combinations of sex genes within the colony have resulted in intermediate types." The male intersexes ("gynandromorphs") of *Acromyrmex* were presumably haploid, all other monstrosities diploid.

It appears that a diploid intercaste may begin development toward the worker end of the series and later deviate toward the female and even across the sex boundary toward the male, while the haploid intercaste starting as a male deviates toward or beyond the female. Thus the diploid intercaste may or may not be an intersex, while the haploid intercaste is necessarily so.

Nothing is known about the behavior of these forms except that two ants, which had a combination of male and female heads with male bodies and genitalia, attempted copulation with workers.

## 6. COLONIES AND NESTS

### SIZES OF COLONIES

Most of the species of gardening ants are small and inconspicuous. Actual counts of the populations of representative colonies are few and incomplete. The gardens in most species contain the vast majority of workers, the brood and the males and females. In theory, it should not be too hard to determine the colony population if the gardens are quickly gathered and the ants counted. In practice, many ants may be missed because the average ant curls up upon capture and looks exactly like the surrounding soil. In *Acromyrmex* and *Atta*, the mobility of the ants means that many will escape under ordinary conditions.

The genus *Apterostigma* appears to have among the least populous colonies of attines. One of *tramitis* had 17 workers and the queen; 20 workers and 12 males were in a colony of *immobile*; 44 workers and the queen of *mayri* were in a Panama nest and 40–50 workers and three females in a Trinidad nest; 133 workers, 21 winged females, and the queen were in *dentigerum* and a few score in *urichi* and *auriculatum* colonies.

One of the two most populous colonies of *Cyphomyrmex rimosus* was found on the shore of the Bay of Panama with 174 workers and 44 wingless females and the other along the Orinoco River in Venezuela with 221–300 workers. Estimates previously had been "a few score" in this genus.

Colony size in the abundant tropical mainland *Myrmicocrypta* was unknown until Nancy Weber carefully collected and counted a colony of *buenzlii* in Trinidad. There were 1,558 workers and two queens. Those missed could have added 10 per cent to the total. Casual inspection of a nest would not have led to an estimate of more than one or two hundred.

### *Sericomyrmex*

Similarly, the estimate in the literature of colony size in the tropical mainland *Sericomyrmex* ranged from the flat statement that there were not more than 200 workers in *S. urichi* to "about 300" in *amabilis*. Mary Lewis collected and counted a colony of *urichi*, finding 1,691 workers. Since then I have kept a colony

(figs. 137, 138) for more than six years and have estimated the population periodically and counted all the natural deaths. The ants fortunately had the habit of bringing their dead to one corner of an empty chamber where they could be removed (table 1).

The colony was collected July 15, 1965 when it then had about 20 workers. It probably started in the preceding late May from one queen. The table shows the deaths of the castes by month and year. The population of workers was estimated to be nearly 1,000 after some 19 months of colony life at 25–27° C and increased to some 2,500 by the end of the thirtieth month. It was believed to stay at the level of some 3,000 workers for more than two years despite the mortality and had a garden of 2,200 ml. throughout.

This prolific queen produced 26,308 ants of the three castes that died through May, 1971. Fully 3,000 workers and a few females remained on the single garden. Males matured later.

In this period 685 females and 6,477 males were produced, a ratio of 1:9.4. The single winged female that appeared in August, 1969, in the midst of a male brood of 3,888 was expected to be followed by others but none appeared in this year. They could not have been overlooked because of their comparatively large size and conspicuous dark brown wings. In 1970 single females appeared in January while the first male pupa was seen in April. Males and females matured in numbers in May and both sexes rested quietly on the garden or moved slowly about as they fed on the fungus.

The maturing of male broods at approximately the same time in three successive years suggests an endogenous rhythm.

### *Trachymyrmex*

Counts of *Trachymyrmex* colonies show lesser populations. The type colony of *ruthae* had 280 workers, 7 winged females, 23 wingless females, and 23 males, and was doubtless low on the sexual forms because of escapes while the colony was being collected. Cole (1939) reported 117 workers, 43 females, and 21 males in *septentrionalis* and one of my students counted 286 workers, 20 winged females, 1 queen

TABLE 1  
DEATHS OF THE CASTES OF A *Sericomyrmex urichi* COLONY BY MONTH AND YEAR\*

Month	1968			1969			1970			1971		
	Worker	Female	Male	Worker	Female	Male	Worker	Female	Male	Worker	Female	Male
January				792	0	10	609	0	0	332	127	304
February				270	0	0	358	1	0	499	92	749
March	625	366	0	835	0	0	482	0	0	256	8	813
April	348	6	0	515	0	8	304	1	0	408	0	48
May	216	0	2	180	0	170	326	0	0	498	0	9
June				193	0	639	96	0	0	339	0	2
July	327	0	119				663	2	92	362	0	9
August	186	0	203	1,013	1	1,377	479	13	1,552	283	0	21
September	163	0	285	428	0	1,335	442	9	863	174	0	31
October	86	0	46	720	0	349	513	15	397	91	0	1
November	400	0	11	561	0	0	345	10	374	195	0	19
December	154	0	0	371	0	0	504	34	371	379	8	399
Totals	2,505	372	666	5,878	1	3,888	5,121	85	3,649	3,816	235	2,405

\*The colony originated May, 1965, and there were no deaths in 1965. Some deaths of workers in 1966 may have been included in the June, 1967, record, when 401 dead workers were removed. No females or males died in 1967. A gap in the table means that no collections were made in that month. One female brood matured in May, 1967, and started to die the following February; the second female brood appeared in early 1970 and lived quietly in the nest for months. The annual male broods matured one or two months before they started to die.

and 32 males in this species. A colony of *urichi* counted by Gary Williamson had 763 workers, 71 winged females, 1 queen, and 562 males, with an estimated 10 per cent missed. In five years a laboratory colony of *zeteki* produced 660 workers and 44 males from 1 queen. At any one time the mature colony consisted of 100–300 workers and in this case the visibility was so good that none was missed.

A record of the deaths by month and year was maintained. In the year of collecting 34 workers died; in the second year, 51; the third year had 22 deaths; then an increase in mortality in each of the next two years to 115 and 116 occurred. In the last full year there were 228 deaths and finally 94 workers died with the queen after about 5½ years of colony life. The monthly mortality until the end varied from 0 to 46.

#### *Acromyrmex*

Colonies and nests of *Acromyrmex* are much larger than those of the preceding genera. The colony of *Acromyrmex octospinosus*, that had the anomalies described in chapter 5, contained 7,166 workers, 175 winged females, and 823 anomalous types or a total, including losses, of fully 10,000 and this would not be a large colony of this species. The order of magnitude of population size in a large *Acromyrmex* colony may well approach 100,000.

The three females of *Acromyrmex octospinosus* alluded to in chapters 4 and 5 were taken immediately after their mating flight on July 1, 1965, and kept successfully in the laboratory. At the end of 12 months there were estimated to be about 150 workers in one, 200–300 ants in the second, and 600–1,000 ants in the third colony. The associated sizes of the gardens are described in chapter 8. June 9, 1967, another female was taken directly at the end of her mating flight. Her progeny and garden were still larger, the workers amounting to an estimated 1,500 at the end of the first year. In the meanwhile, the three 1965 colonies continued to thrive variably. At the end of the third year the first colony had expanded to an estimated 2,600 workers, the second to 2,050 and the third to 3,600 workers.

The variable history in the laboratory of these and other colonies in other species is undoubtedly reflected in nature, as the data of Autuori and Amante show in the Brazilian *Atta*. The colonies do not grow at a simple rate but each is affected by its own set of environmental factors. The internal situation also varies, such as the vigor of the individual queen and the effectiveness and size ratios of the workers.

#### *Atta*

The collecting of the adults of an entire, mature *Atta* colony in South America is a formidable undertaking and most investigators



have been content to make estimations, which usually run into the hundreds of thousands.

Autuori (1956), however, counted the sexual individuals in a nest of *Atta sexdens* of 47 months, digging up the colony on the day before the second nuptial flight of the sexes was to take place. He thus secured the entire sexual brood. There were 43,820 winged males and females, 38,481 being male and 5,339 being female, a ratio of 7.2 to 1.

The most comprehensive collections of worker ants from an *Atta* nest appear to be those of Martin *et al.* (1967b) from *Atta colombica tonsipes*. In all, 6.35 kilograms of ants were collected. About 65 to 85 per cent of the colony was estimated to have been taken. The colony therefore may have amounted to 7.48 to 9.78 kilograms of ants. Random samples ranged from 4 to 8 milligrams per ant, indicating the colony had 1.0 to 2.5 million ants. It was realized that the ants which escaped collection in this manner were largely the smallest workers. The largest soldier measured was 14 mm. and the smallest worker 3 mm. The nest was about 8 meters in diameter and was in Panamanian forest. Although the crater system of the nest was much smaller than that for a nest of *Atta sexdens rubropilosa* of 6 years and 5 months age (Autuori, 1947) it may well have been of roughly comparable age. The Autuori nest had 246 fungus gardens. The above population estimations may well be raised on the basis of counts made below in an *Atta cephalotes* nest. The Panama nest may well have had 2.5 to 5 million ants. The basis for this statement is the probability that nearly all of the minima workers remained tightly curled up with the garden fragments and were not collected in the 6.35 kilo sample.

I took the direct approach to determine the worker population in an entire representative

garden of a laboratory colony of *Atta cephalotes*.

The chamber with garden and ants was separated on March 17, 1970, from the remainder of the colony, which at this time had five gardens, containing an estimated 6,800 milliliters. The colony was one taken in Trinidad on July 13, 1965, when it was then estimated to be about one year old. The queen was in another garden in 1970 and the one separated had no brood. The gardens had always been maintained on fresh, leafy substrate, as in nature.

The garden and ants represented a natural biological unit of the colony and all ants present were those naturally in attendance on the garden. The separation was such that none escaped. The net weight of the garden and ants was 235.55 grams. The volume of the garden was 1,700 ml. The volume per gram was 7.2 ml., compared with ratios of 8:1 and 9:1 in other laboratory gardens of this species and was the same for one determined in nature in Trinidad.

All ants in the garden were systematically removed, counted, and measured. At first they were allowed to leave from tubes attached to openings in the plastic chamber at a controlled rate so that none was lost. These included a high proportion of the 4 and 5 mm. lengths. The entire population of workers could only be taken by removing the garden piece by piece, after the aggressive ants left in the early stages of collection. The minima sizes generally remained to the last and finally were found by painstakingly scrutinizing every part of the garden. In many cases they were tightly appressed to the substrate and remained motionless. It is these smallest sizes that may well have been partly missed in such samplings of chambers as those of Goetsch (1939) and Weyrauch (1942).

The results to nearest mm. were:

Size in mm:	1.5	2	3	4	5	6	7	8	10	12
Numbers	173	3,493	1,718	1,737	1,135	367	93	28	17	1

There were 8,762 workers, divided into minimas (1.5–3 mm.) 5,384 or 61 per cent, medias (4–6 mm.) 3,239 or 37 per cent, maxima workers (7–8 mm.) 121 or 1 per cent and soldiers (over 9 mm.) 18 or less than 1 per cent. The latter per cent will vary markedly in gardens and from time to time according to the position of the garden and age of the colony. A nearby sister colony at the same time had 42 soldiers in

a tube one meter long that was leading from the laboratory table to the first of several gardens on an upper level. Generally the soldiers tend to congregate at the gardens nearest the entrances. This census of ants in a representative garden of known weight and volume provides data that may be used generally to estimate colony population wherever the numbers, sizes, and weights of gardens may be determined. The



FIG. 77. Entrance to the nest of *Mycetophylax conformis*, an ant of the Caribbean seashore. The ants form a circular crater repeatedly after the wind and rain have erased the former one. Trinidad.

assumption, based on observations over the years, is that gardens of a given size can only be maintained by a given population. This has proven true in observation nests of many small species of different ant genera where the ants could be counted directly in attendance on the gardens.

In a sample of 6,105 workers from four gardens of *Atta cephalotes* taken from a nest in nature known to be two years old there were 3,942 ants or nearly 65 per cent of the minima sizes (1.5–3 mm.). The other sizes were similar in proportion to those in the census of 8,762

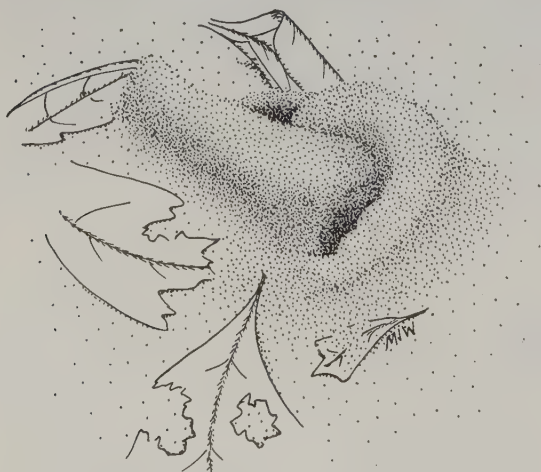


FIG. 78. Irregular ridges of fine clay soil thrown up in the formation of the nest of *Myrmicocrypta ednaella*. Panama.

ants. The two-year-old nest was estimated to contain 250,000 to 300,000 ants based on the numbers of gardens exposed under a square meter in the center and the above sample count from fractions of four gardens.

Indirect evidence on the populations of young captive *Atta cephalotes* colonies includes the recovery of 1,800 ants drowning in a moat surrounding a colony of 11 months in age. The loss did not slow up the steady growth of the gardens. Young *Atta sexdens* colonies that originated in May 1970 had populations of about 50 workers each on July 15. By the following March 12 each had an accumulation of some 500 naturally dead workers, mostly of the 2 to 4 mm. sizes,



FIG. 79. Crater entrance to nest of *Trachymyrmex septentrionalis* showing the way in which the ants march out from the central hole for a distance of about 10 cm. before dumping the sand grains to form a ridge in semicircular form. Florida.

and several thousand active workers with expanding gardens.

## THE NEST

### EXTERNAL APPEARANCE

The external appearance of the nest tends to be different according to the species (figs. 2, 81, 82, 86). The smallest and most primitive ants such as those of *Cyphomyrmex* and *Apterostigma* have only a bare hole as an entrance and this could be a crack in rotted wood. The tropical *Myrmicocrypta* (fig. 78) and *Mycocepurus* pile up the fine grains of soil to make irregular and sometimes furrowed heaps. These are distinctive generic characters.



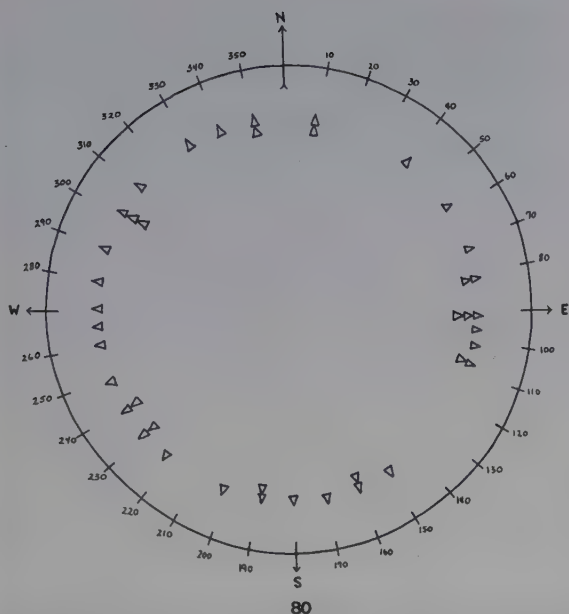


FIG. 80. The points of the compass with triangles showing the direction of the entrance to the nest of *Trachymyrmex septentrionalis* from the horns of their semi-circular craters. 41 nests are represented and they avoided pointing to only a small part of the southeast. Florida.

A characteristic entrance to nests of most species is in the form of a symmetrical low crater. The craters may be suggestive of a coral atoll, flat in the center and with a low rim. The hole is usually in the middle. It is an interesting situation that in different species the ants march out from this hole for a certain distance, short in the smallest ants and longer in larger ants,



FIG. 81. Entrance to the nest of *Trachymyrmex wheeleri* in the form of a raised crater which could be easily washed away by rain. The forceps are 113 mm. long. Colombia.

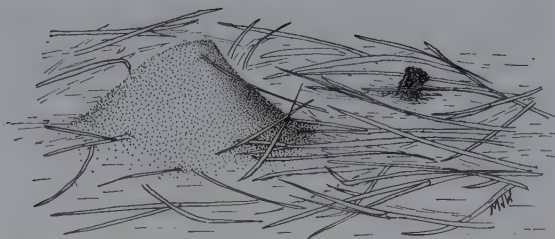


FIG. 82a. Turret entrance at right to the nest of *Acromyrmex (Moellerius) landolti (balzani)* of authors on the llanos of Venezuela, where the ant is an important pasture pest. The ants have marched out with sand from excavating to create a conical mound at the left.

before dumping the soil. Why they will go out evenly in all directions to create a 360° circle has never been explained. In the northernmost species they do not do this, but create a rim much higher in one direction than in the others so that it is half-moon shaped (fig. 79). An examination of many nests in Florida to see whether the higher part of the crater was always or most always in one direction of the compass revealed that all directions were used if enough nests were found (fig. 80).

The seashore crater of *Mycetophylax conformis* (fig. 77) is a particularly good example of repetitious crater making since its craters of loose sand are readily blown or washed away. The crater is circular and has the entrance centrally located. It is a distinctive generic character. One entrance in Trinidad during the rainy season was 1.5 mm. in diameter and the ants marched 20 mm. away to deposit their sand



FIG. 82b. The turret of the mound shown in fig. 82a in greater detail showing a collar of *Trachypogon* grass sections and part of the funnel exposed at the left.





FIG. 83. Habitat of the census of the nests of *Acromyrmex* (*Moellerius*) *landolti* *balzani* (fig. 115). The conspicuous mounds are those of termites (*Amitermes*) on the Rupununi Savannas, Guyana, with the Kanuku Mountains of the Guyana Highlands in the background. These mounds have been wrongly labeled those of "Coushi" ants (which are *Atta sexdens* and *laevigata*) in post cards for sale in the capital of the country. The nest of *sexdens* is usually near or under trees of the forest and that of *laevigata* under single trees or bushes out on the savannah. In the dry season the grass is regularly burnt by the ranchers or eaten down by cattle. A third *Atta* (*cephalotes*) inhabits gallery forest on the slopes of the mountains.

Termites, these *Atta* species and the *Acromyrmex* are the primary animals in reducing the lush vegetation during the rainy season here. The latter ant and mound-building termites may share in cutting the same grass clumps about their interdigitating nests.

grains. Another entrance was 3 mm. in diameter and in the center of a crater 66 mm. in diameter. A third nest entrance was 4.5 mm. Intermittent showers on this day were frequently washing all craters away. As soon as a shower would pass, 3 to 6 ants would emerge to clear the entrance. During the dry season no crater could be formed because of the constant trade winds. Daily crater variation in one *Trachymyrmex* nest is known (Weber, 1969c).

The crater formed by the semi-desert *Mycetophylax emeryi* in the Sierra Chico of Argentina was flat and mostly blown away because of the winds. The entrance was central and the dimensions of the crater and entrance were much the same as those of the Caribbean species nearly 3,000 miles to the north.

The craters of the Trinidad *Sericomyrmex urichi* are flat and unusually large for the size of the ants (fig. 114). They are irregularly circular and the ants tend to use one part of the

crater at a time for excavated soil so that sometimes, if there is a lag in excavating, part of the soil becomes bleached and pale while fresher soil in the circle is a contrasting red color. The soil craters of *Acromyrmex* (*Moellerius*) *landolti* tend to be semi-circular but they have also a turret entrance (figs. 82a and b, 91). Here again, the ants march out with the soil from excavating and dump it at a fixed distance from the entrance. In grasslands the excavated crater soil is hidden in the grass some distance from the crater and this behavior may have survival value. The craters of *Atta* are the largest and highest in attines.

Next in development to the crater is the turret or chimney (fig. 84). It is common among the three highest genera. The turret in the smaller species may be only an inch or two (2.5–5 cm.) high. Since tropical rain-forest soil is usually



FIG. 84. Early stage in the formation of a new nest of *Atta cephalotes* in Trinidad. The first broods have erected a 12 cm. turret of wet clay grains above the single garden of this stage. The soil has been excavated to show the garden.



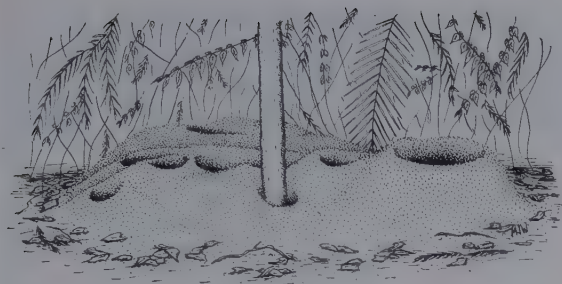


FIG. 85. The mound nest of *Atta cephalotes* in the Nariva Swamp, Trinidad, consisting of fused craters.

moist and often laterite or clay, the particles of soil stick together. Often the turrets resist rain for a time or they may be placed in sheltered places where they are not affected. An oddity in Guyana was a species with an ear-shaped turret (Weber, 1946). If the ants are nesting on a slope, the turret may start out at an angle but will immediately take a vertical position, indicating that the ants have a sense of gravity. It is not that a turret at an angle will fall down since tropical wet clay is tenacious. Where *Atta* nests on sandy soil the turrets may disintegrate quickly from rains or winds.

The new queen in *Atta* will form a smaller crater when she first digs into the soil after her nuptial flight. The entrance is large because she is large and is a good indication of the genus. The crater is similar in *Acromyrmex* but the hole is much smaller since the female is smaller. The crater becomes a turret by the activity of the first broods of workers about 50 days later. This grows slowly up to the 80th to 90th day in *Atta sexdens* according to Brazilian investigators. By the 150th day it has reverted to a crater shape and from then on, throughout the years of the colony, only craters are formed. The craters crowd one another and the numbers



FIG. 87. Unusual garden (40 × 30 mm.) of *Cyphomyrmex longiscapus* suspended from twigs above the soil level and covered by the ants with mud. The site was a deep, moist ravine in the Andes of Colombia.

increase with the increase in colony population (figs. 85, 86).

From six to nine months after the start of an *Atta cephalotes* colony the turret becomes a crater of growing height because of the increase in soil from excavation. This is dumped in the immediate vicinity of the nest entrance and usually on all sides. The nest now increases to three or four chambers and several thousand workers will have been produced.

The second half of the first year of colony life is marked by the addition of one or two or more new craters in the size range of 20–30 cm., each surrounding new nest entrances. Autuori (1942) characterized the first year in *Atta sexdens* as the infantile phase, with about 10 entrances.

A score or more of craters and entrances may characterize the nest at the end of the first year and one-half. This is the juvenile phase of Autuori and the nest entrances may grow from 10 to 1,000.

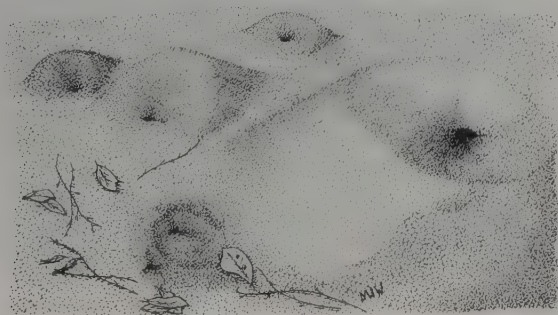


FIG. 86. Detail of the craters of a nest of *Atta sexdens* along the Orinoco River, Venezuela.





FIG. 88. A small colony of *Apterostigma mayri* Forel in the fallen husk of a fruit of greenheart (*Nectandra Rodei*). The forceps are 113 mm. long. Guyana.

Jacoby (1944) divided the early nest history of *sexdens* into the small crater (40th day after fecundation), the turret stage (40–120 days) during which there are two chambers, and the three chamber stage from the 150th day. Betancourt (1941) devised a mathematical formula to estimate the age of the colony from the nest entrances. The mature stage has been reached when the nest has about 1,000 entrances and the sexual brood is produced. Autuori found that there were 53, 63, and 113 entrances to three nests at the end of two years which increased to 1,071, 853, and 984, respectively, 14 months later.

The mature *Atta* nest is a conspicuous feature of the landscape and consists of many craters which, as they disintegrate, form a large but low mound. They are a major feature of the grasslands, especially of parts of Brazil. Amante (1967b) recorded 18 fully mature nests per hectare and as many as 64 of variable sizes per hectare in one area. The nests are less con-

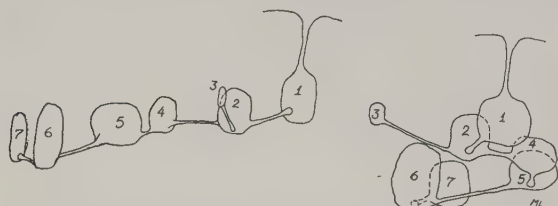


FIG. 89. Nest of *Sericomyrmex urichi* in side view (left) and in front view (right) as determined by excavating the 7 chambers. Trinidad.

spicuous in tropical forests but may be the only raised feature of the soil in otherwise level areas. The nest architecture is described below.

On the pampas of Argentina, Uruguay and Brazil there are several dome-making species of *Acromyrmex* whose nests of thatch are not especially oriented towards the sun but whose brood and garden is kept in the same upper part of the nest that unrelated ants with a similar nest use in the north temperature zone (figs. 95, 96, 97, 98).

One of several *heyeri* in Uruguay (Weber, 1966a) (fig. 104) was 54 × 52 cm. in basal diameters and the all-thatch mound was 18 cm. high. These were superficially like mature mounds of *Formica obscuripes* in North Dakota and the thatch also consisted of grass and herb stems.

A thatch nest of *Acromyrmex ambiguus* on the pampas of Argentina was 17 cm. above the general soil surface and had a broad base of earth of 122 cm., on which was the thatch part



FIG. 90. The garden of *Trachymyrmex wheeleri* showing the lamellate structure. Forceps 113 mm. The chamber was at a depth of 12 cm. and there was a second chamber 15 cm. below the first. Colombia.





FIG. 91. Two of several gardens of *Acromyrmex* (*Moellerius*) *landolti* (*balzani* of authors) under *Trachypogon plumosus* grass. Llanos of Venezuela.

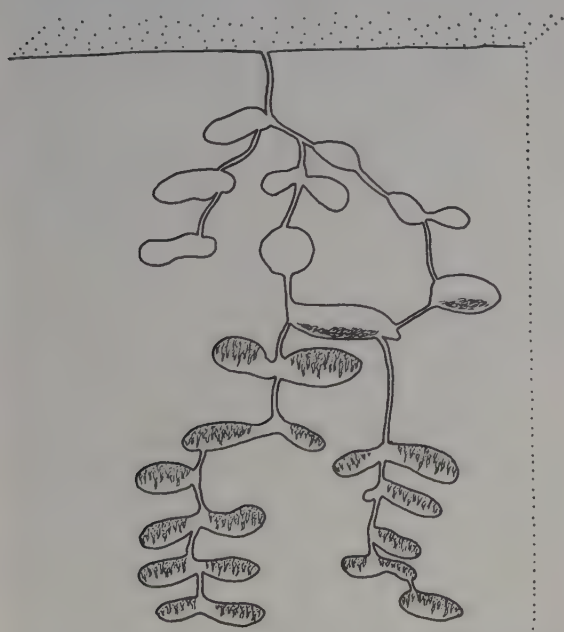
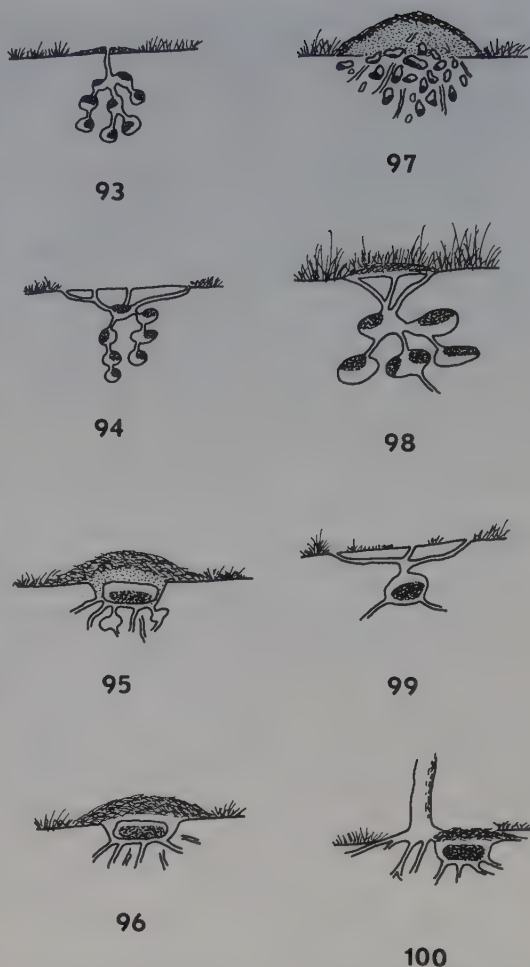


FIG. 92. Section of the nest of *Acromyrmex* (*Moellerius*) *silvestrii* Emery of Argentina after Bruch. Numerous gardens are suspended from the ceilings of the deeper chambers. Above them are two chambers with refuse and the most superficial chambers are empty.



FIGS. 93-100. Sections of the nests of species of *Acromyrmex* in Argentina and Brazil after Bonetto. (93) *fracticornis*; (94) *striatus*; (95) *heyeri*; (96) *hispidus*; (97) *lobicornis*; (98) *ambiguus*; (99) *lundii*; (100) *coronatus*.

70 cm. in diameter. This type is also represented in some *Formica* nests of the north.

The tropical *Acromyrmex*, like *hystrix* and *octospinosus* form much more irregular nests (Weber, 1945, 1946). They nest quite commonly up in trees or on the top of a large fallen tree trunk in tropical rain forests. One of *octospinosus* nested in the crown of a palm in the Port of Spain Botanical Gardens in 1935. The smooth trunk of the palm was 8 meters high and from 8 to 11 meters was the crown where the ants had gathered debris to form their nest. It was quite invisible from the ground but the files of the ants carrying leaf and flower sections were conspicuous as they crawled up the trunk



FIG. 101. Diagram of the nest in section of the mound-building *Acromyrmex lobicornis* of Argentina after Bonetto. Scattered cells contain fungus gardens. The mounds are reminiscent of the Holarctic ants of the genus *Formica* and conserve heat.

from neighboring trees. One of *histrrix* was in a mass of aerial roots of plants at the base of a tree, the mass being 174 cm. high and 150 cm. at the base (fig. 102, 103). Other nests of both species may be inconspicuous under trash on the ground.

#### INTERNAL ARCHITECTURE OF NESTS

The large surface area covered with craters and the great volume of sub-surface soil occupied

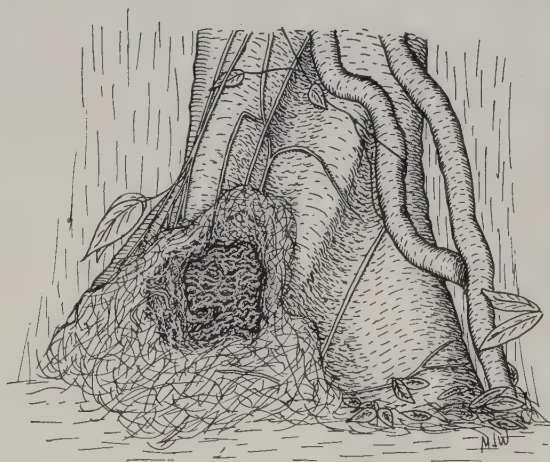


FIG. 102. A nest of *Acromyrmex histrrix* in Venezuelan rain forest consisting of a single garden under a pile of trash at the base of a tree with lianas.

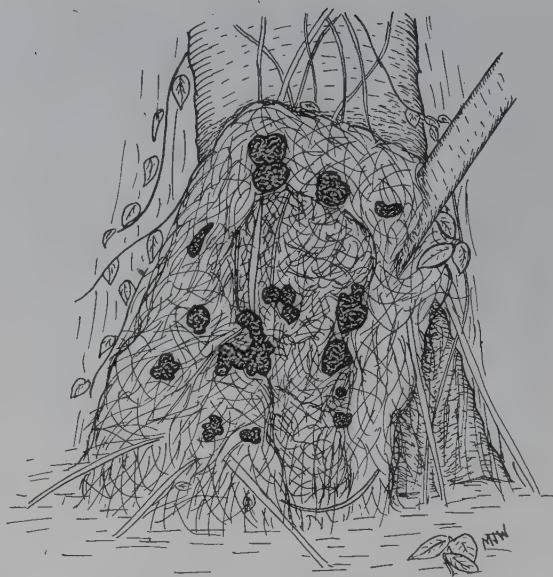


FIG. 103. Another nest of *histrrix* in Guyana with many small gardens.

by the chambers of the mature *Atta* colony obscure the general plan of attine nests. These are much simpler, as the smaller populations of ants would necessitate.

The simplest of all is the irregular, pre-formed cavities occupied by the yeast-culturer, *Cyphomyrmex rimosus*. Its nests may be in soil, under bark of rotted wood, in humus about roots of epiphytes as high as 30 meters in a 60-meter tree in rain forest (one record in Guyana), or in a snail shell on the ground.

Other species of the genus like *bigibbosus* also nest in soil or in humus among roots of epiphytes. The nest of the type of *C. longiscapus* in Colombia was unusual in being in the form of a sack of



FIG. 104. The mound nest of *Acromyrmex heyeri* on the Argentine pampas. Test tube 147 mm. long.



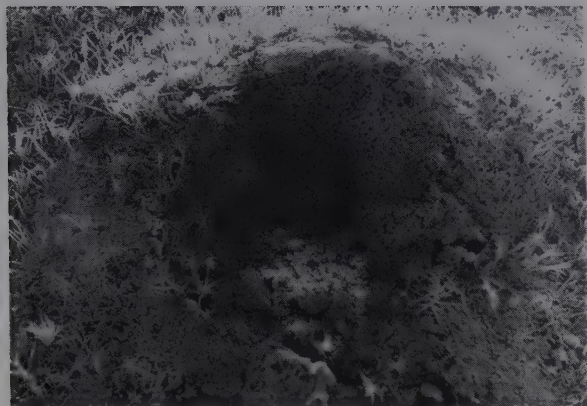


FIG. 105. Colonies of three social insects nesting together in Rio Grande do Sul, Brazil. The garden of *Acromyrmex* (*Moellerius*) *heyeri* is in the center of the mound, the fire ant, *Solenopsis saevissima*, and the termite that made the mound surround the attine.

agglutinated humus suspended from rootlets in a densely forested steep ravine (fig. 87). The covering was 2–7 mm. thick and surrounded a single garden 40 mm. high and 30 mm. wide.

The nests of small ants such as *Mycocepurus*,



FIG. 106. The process of forming a new garden in a mature nest of *Atta cephalotes opaca*. The ants excavate the new chamber, leaving roots intact, then bring in particles from a nearby mature garden and attach them to the roots. Soon the new garden will nearly fill the chamber. The forceps are 113 mm. long. Colombia.



FIG. 107. Superficial part of the nest of *Atta cephalotes* on the edge of a plantation in Trinidad. The ants of some *Atta* commonly nest at the margin of fields. Knife 10 inches (25 cm.) long.

*Mycetophylax*, and *Myrmicocrypta* are of one or several chambers in the soil. The tunnel entrance of *Mycocepurus tardus* was less than 1 mm. in diameter and led irregularly to a 20 mm. chamber at a depth of 205 mm. That of *Mycetophylax conformis* on the Caribbean seashore was similarly tenuous and led by a tortuous route to a total depth of 650 mm., having several small chambers branching off en route. The nests of *Myrmicocrypta buenzlii* consisted of one or several chambers of comparatively large size, some 100 mm. in diameter, and at depths of 25 to 90 mm.

The nests of *Apterostigma* rarely may have a crater entrance (*mayri*) but usually the entrance is an inconspicuous bare hole in the soil or rotted wood in which they nest. One nest of the common *mayri* had the single chamber about 7 cm. in diameter and at a depth of 45 mm. Another was in the fallen husk of a greenheart



FIG. 108. Superficial part of the nest of *Atta insularis* in Cuba showing a few of the numerous fungus gardens.



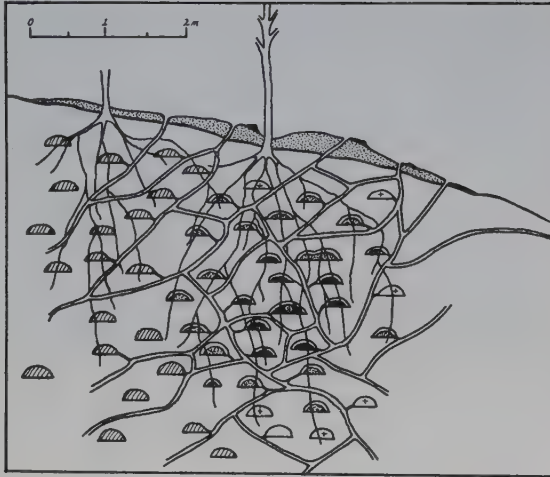


FIG. 109. Diagram of the nest of *Atta sexdens* in Brazil, after Eidmann. There is one female in a central chamber surrounded by other chambers (solid black) with brood and most of the rest of the chambers contain fungus gardens. In many other cases the sides have more regularly ascending tunnels.

fruit (fig. 88). Others were barely beneath the hard shell of rotted wood branches or tree trunks. Common sites include the humus at the base of epiphytic plants.

The nests of *Sericomyrmex* generally resemble those of *Trachymyrmex*, sometimes having one to eight chambers. One of *harekulli* had the first chamber 85 mm. high by 95 mm. broad that was at a depth of 200 mm. The next was at a depth of 380 mm. and the third was 500 mm. deep. A nest of *urichi* had seven gardens at depths of 10 to 22 cm. (fig. 89). The chambers containing the garden varied from 3 cm. to 12 cm. in height and 5 to 9 cm. in diameter.

The nests of the small species of *Trachymyrmex* such as *bugnioni* have correspondingly small chambers, one colony having a 20 mm. single chamber at a depth of 200 mm. Slightly larger species, such as the widespread *cornetzi*, may have a turret entrance and a main chamber some 45 mm. in diameter at a depth of 70 mm. The chamber made initially by the new queen will be more superficial. The larger species (fig. 90), such as the widespread *urichi*, may have multiple chambers in a vertical series. One of *urichi* had 5, one above the other to a depth of 30 cm.; another had 6 chambers at depths of 2.5 to 27 cm. They were from 3 to 12 cm. in diameters. One of *zeteki* had a single chamber at a depth of 80 mm. that was 80 mm. broad and 60 mm. high. Such rather shallow nests of a

single large chamber may occur in other species but more commonly as the colony grows more chambers will be added and at greater depths. In the northern *septrionalis* these in some cases are in a vertical series while in others they branch off at several levels (Wheeler, 1907, 1911; Cole, 1939).

The internal architecture of mature nests of *Acromyrmex* often differ markedly from those of *Atta* despite the general similarity in habits of the ants (figs. 92–100). Several score fungus gardens (amounting to some 30 liters) were scattered in the well-aerated pile of humus and roots of the *hystrix* nest mentioned earlier (fig. 103). Other nests in the soil are much smaller and simpler and appear to lack the organization of *Atta*. That of *lundi* is noteworthy in having a large chamber one-half meter or more in diameter in addition to numerous smaller chambers spread laterally. Diagrams of this and other species are shown by Gonçalves (1961) and Bonetto (1959) (fig. 101). The mound builders have a large central chamber under a few centimeters of thatch cover. The two thatch nests of *heyeri* described above had each a 5 cm. thatch cover under which was a single, centrally located large chamber about 20 cm. high and 34 cm. wide. The thatch mound of *ambiguus* noted earlier had a single centrally located, but irregular, chamber that was 47 cm. vertically and had a width of about 37 cm.

The nest of the ants of the subgenus *Moel-lerius* of grasslands is more like that of a large *Trachymyrmex* but with chambers of greater

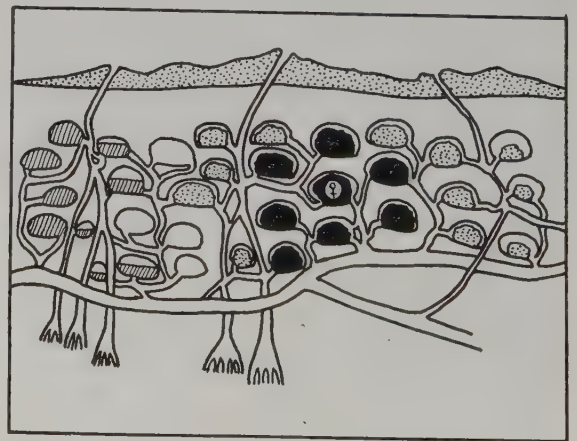


FIG. 110. The Peruvian nest of *Atta sexdens*, after Weyrauch. A large canal at the base of the chambers is an adaptation to a higher water table than shown in the Brazilian nest of Eidmann.

size. Bruch (1917) figured one of *silvestrii* (fig. 92) that consisted of three vertical series, two with 11–15 chambers, some of them forming opposite pairs. The widespread *landolti* nest may have three or more chambers in a vertical series (fig. 91).

#### THE ATTA NEST

Excellent diagrams of the mature *Atta* nest in surface view and in section have been published by South American authorities (fig. 109, 110). Brazilian investigators have examined *Atta sexdens rubropilosa* nests particularly, and those of this species and *cephalotes* have been the general subjects of economic investigations. Amante (1967) compared the nest architecture of *capiguara* with other species in the same area. Bruch's figures (1917a) of a large nest of *vollenweideri* in section was used by Wheeler and Forel in their widely distributed books. In recent years nests of the United States species have been well described by Moser (1963, 1967) and Neelands (1959).

Chambers tend to be excavated on all sides of the first chamber with the queen remaining in the center. In a two-year colony of *cephalotes*, where craters occupied eight square meters, beneath the surface the chambers spread out horizontally in hard clay. Forty were estimated to be in this nest and twelve were excavated beneath one square meter in the center. The deepest of the twelve was 14 cm. down and the most superficial was 8 cm. There were connecting tunnels of 2 to 3 cm. in diameter.

The gardens that contain brood tend to be centrally located and in chambers surrounding the queen chamber. The most peripheral gardens tend to be the newest and ordinarily contain only the adult workers.

#### *Drainage and Ventilation of the Atta Nest*

A detailed examination of the canal system of nests of *Atta sexdens rubropilosa* in Brazil was made by Jacoby (1944, 1952–1953, 1955). He poured cement down nests and determined the architecture of nests of various ages by removing the soil from the casts. The tunnels entering and leaving each chamber regularly are located at the base. This long-known feature always hindered attempts at forcing poison gas or liquids into each chamber. At the same time each garden in its chamber needs abundant

circulation of air for the metabolism of the fungus as well as the ant brood.

The most important element in this circulation is a lateral system of large canals located on the periphery of the nest. These slope down to the middle and converge at the bottom here. It is these lateral canals that bring fresh cool air into the nest at night. An intricate system of smaller, irregularly vertical canals occupies the middle of the nest and the air ascends in these. Forcing poison gas down this inside canal system is useless since the circulation works in the opposite way. Instead, poisoning should be done in the lateral system.

Weyrauch (1942) showed a different arrangement in Peru (fig. 110). The central, more or less vertical, canals continued down to the water table and permitted the ants to get needed water for their gardens in time of drought. He showed one very large horizontal tunnel at the base of the entire chamber area instead of a larger and more peripheral system of canals. Perhaps the circulation of air in mountainous areas is less of a problem than that in flatter country.

A still different architectural form is shown by Amante (1967a, 1968) in *capiguara* nests. The central area of mature nests is occupied by a few more or less vertical canals which expand at the base into cone-shaped spaces of large size which are used for storage of refuse. The surface of this central area is characterized by large mounds of loose soil. To force poison down these central canals is a waste of time and material. The periphery of this Zona Morta (dead zone) contains the active, living part of the nest, the Zona Viva. Here are the gardens and the brood. These are connected with each other and to the central chambers by small canals.

The mature *cephalotes* nest was shown by Stahel and Geijske (1939) to have features of the other species, including large but irregular waste chambers. The mature *texana* and *vollenweideri* nests (Moser, 1963; Bruch, 1917a) were similar, Bruch showing one large central refuse chamber.

Subterranean tunnels reach an unusual development in *Atta texana* as shown long ago by McCook (1909). He measured one that was at an average depth of 18 inches (46 cm.), and an occasional depth of 6 feet (1.8 m.) but that extended 448 feet (136 m.) entirely beneath the earth. Such tunnels in the territory of *texana* enable the ants to reach suitable plants without



exposing themselves or the cut leaf sections to much dehydration. Buckley a century ago even thought that they tunneled under a stream to reach vegetation, something never proved.

Another type of tunnel may form in tropical rain forest where an ant path on a slope may be a site for erosion from heavy rains and gradually sink into the soil (Weber, 1946) (fig. 119). Superficial roots and fallen debris may gradually cover such a trench and convert it to a tunnel.

#### TEMPERATURES WITHIN THE NEST

The ants, extending as they do, through the temperate and tropical zones, are faced with a great range of potential temperatures. They themselves and their fungi have no internal control over temperature and the ants can only regulate this through their nests and through their activities, such as foraging at particular times. The following temperatures indicate some of the extremes under which they and their fungi exist.

Among the limited data for the maximum temperature at the nest are those for the arenophilous *Trachymyrmex septentrionalis* in south central Florida. Here in the summer the crater surface reached a temperature of 53.7° C at 12:15 P.M. At the depths below were these maxima:

10 cm.	36.9°
20 cm.	32.5°
30 cm.	30.9°
40 cm.	29.8°
50 cm.	29.6°

The gardens were mostly at depths of 20–40 cm. in this period. Average summer crater temperatures at sunny sites were 30–35° C, cooling to 25–29° C at garden levels.

Temperatures in New Jersey colonies in other seasons are given below under hibernation.

#### *Temperatures in a Nest with Mound of Thatch*

The mound-building *Acromyrmex* of the southern hemisphere illustrate adaptation to low temperatures that are unique in the attines.

*Acromyrmex ambiguus*, as noted earlier, has a mound of thatch and this creates markedly warmer conditions for the fungus garden. This species appears highly local and uncommon and is found in south Brazil, Uruguay, and Argentina. A nest was excavated late winter, August 12 (Lat. 34°30' S.), and was on the black earth amid short grass and herbs. Some eight run-

ways converged on it from all directions (fig. 117). These were sunken in the soil and gave protection to the ants besides holding the warmth better than open soil. The mound above the general soil level was almost entirely thatch with little soil. Soil from the excavation of the large central chamber, which extended below the general soil level, had mostly blown away.

Temperatures were taken at midday. The air temperature was 28.0° C at a height of 1 meter and the surface of the surrounding soil was 24.6°. The surface of the thatch mound was 18.3°; at a depth of 10 cm. in the thatch it was 22.8°. The surrounding soil at 10 cm., however, was 13.0°. The contrast between the nest and the surrounding soil was even greater at 20 cm., being 12.2° in the soil when it was 28.5° in the garden. Only a colony of many thousands of large and vigorous ants could create such an incubator and food chamber. The single garden in this case was 37 × 37 cm. in maximum dimensions.

Other temperatures of Argentine ants themselves are given below under Reactions to low temperatures (p. 71).

#### *Temperatures in Atta Nests*

The climate in the *Atta* nest in tropical America reflects the temperature of the surrounding soil except as it is modified by ventilation. In the tropical moist forest the constant high relative humidity as well as constant warm temperatures tend to reduce these variables.

Representative lowland tropical conditions exist in the Panama Canal Zone where in March, June, and December at the same hours the shaded subsurface clay soil of *Atta colombica tonsipes* nests, at depths of 10, 20, and 30 cm. was essentially isothermal, 26° C ± 0.3° (Weber, 1959). The surface of the soil was slightly warmer, while in nests situated where the sun shone it was of course much higher. In such clearings in the forest the temperature at depths of 10, 20, and 30 cm. showed a range of 30–33° at 10 cm., 29–32° at 20 cm., and 28.5–32° at 30 cm. at the same time but this would have been affected by the amount of insolation during previous hours. This would not apply to sites in the shade of the forest where the surface remains close to 25–27° throughout the year at all hours.

At a depth of 20 cm. in the main tunnel of an *Atta* nest a low of 24.3° C was recorded which was thought to be the effect of ventilation.



Eidmann found that the temperature of the fungus chambers in Brazil (Lat. 22° S.) *Atta sexdens* nests at varying depths and times of day was 25° C ( $\pm 4^\circ$ ). The relative humidity was 56 per cent ( $\pm 2.5^\circ$ ) in the months of September to early November, 1933. The isotherm rises here from 20° in July to 26° in January.

#### REFUSE DEPOSITS

A somewhat variable situation in the nest of *Atta* is the specialization of certain chambers to receive exhausted substrate or other refuse such as dead ants, as mentioned above under internal architecture (p. 60). South American investigators, writing in German, have referred to a particularly large cell, the "abraumgruben" (rubbish pit or hole) of huge size as being used in part for an air space and in part for refuse. They figure one cell with a length of 160 cm. and another with a man in it. A large Brazilian one measured 120  $\times$  90 cm. At first it was thought that these were always old fungus chambers. Later study showed that the size of the chamber, far larger than ordinary garden chambers, ruled out that explanation. They have been shown to be used primarily for exhausted substrate and to harbor many organisms. They are also used as burial chambers for the ants that die normally in numbers in a large colony.

A similar adaptation to the disposal of exhausted substrate is known in *Atta texana* (Moser, 1963), where the chambers are smaller and less regular.

The flexibility of these ants is shown by the fact that they can both store old substrate, a dangerous commodity because of its likelihood to develop toxic bacteria, other fungi, or harmful animals, and cast it out on occasion. An *Atta colombica tonsipes* colony in the Panama Canal Zone was observed in June of 1954 and 1955 and March of 1957 to cast out great quantities of clean, golden-brown exhausted substrate several meters away from the nest, carrying it over the same large smooth rock and letting the pellets roll down below (Weber, 1956c, 1969b). The files were as dense with workers as a leaf-carrying file. Each year the pile was more than two liters. It was, of course, casting out exhausted substrate at many other times but March and June may have been months when the exhausted substrate from the dry season was being cast out as the gardens were being renewed with fresh leaves. Another colony of

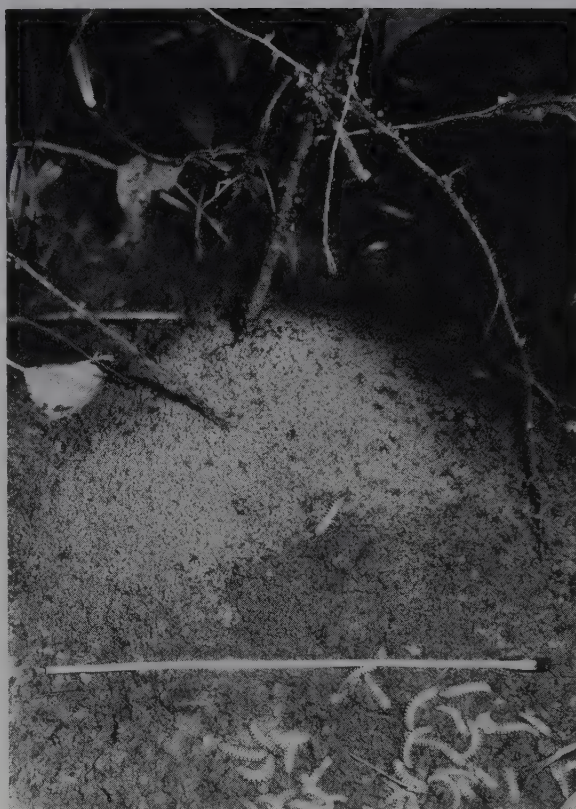


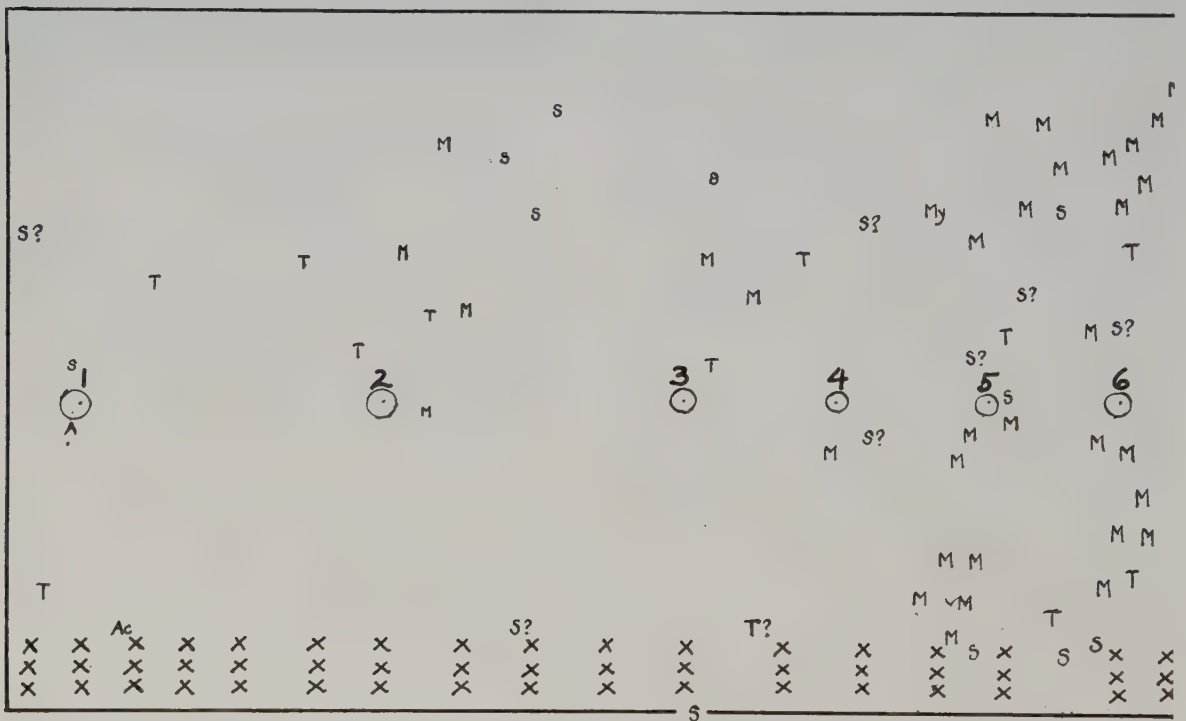
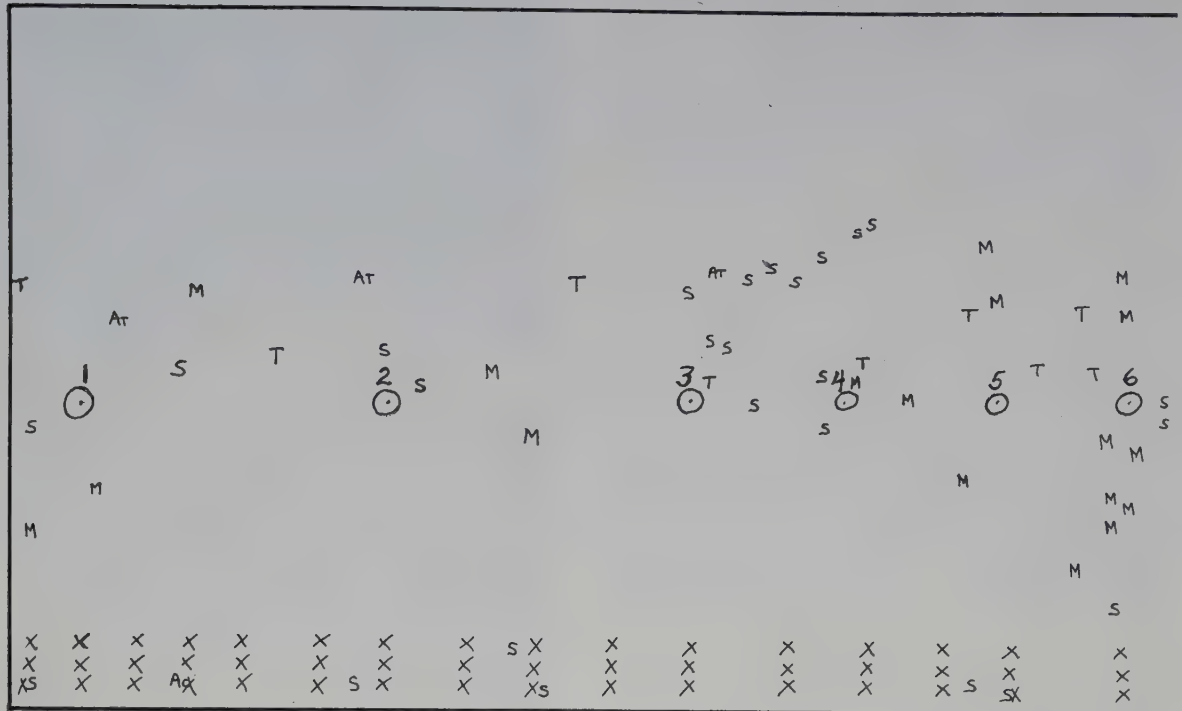
FIG. 111. Pile of exhausted substrate cast by *Atta* at the base of twigs in Costa Rica. The tape is about 48 cm. long including the case. Millipeds have aggregated at the base and are feeding on the refuse. (Phot. C. W. Rettenmeyer.)

*tonsipes* here had been carrying the refuse up a tree trunk at the edge of the nest, then letting it drop below to form a cone about the base of the tree that was also several liters in bulk. A Costa Rican refuse pile is shown in fig. 111.

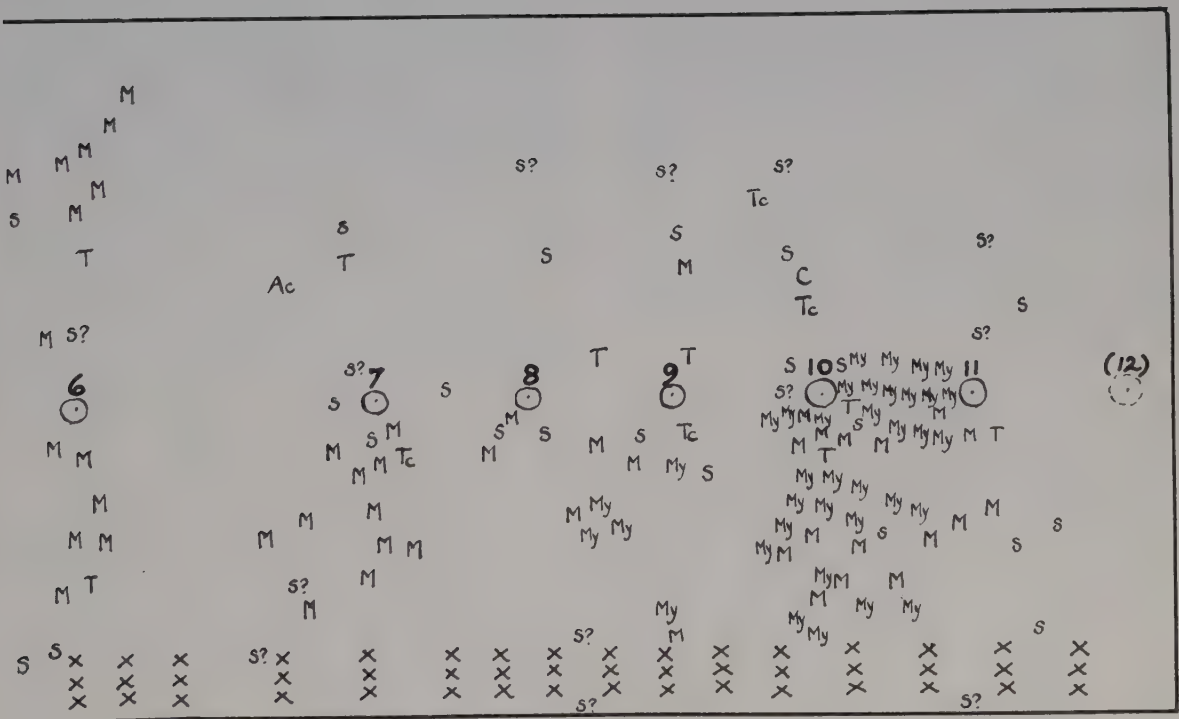
Whether the exhausted substrate and dead ants are buried in refuse chambers or are cast outside in certain areas, the material attracts other organisms. If the material is buried, it does not dry out and can support a miniature world, an ecosystem of its own. There will be fungi and bacteria to break down the plant material, vegetarian animals to feed on this, then a series of predators and parasites.

#### COLONIES IN A LIMITED AREA

A study initiated on the campus of the University of the West Indies in Trinidad in 1964 (Weber, 1966b) provides an illustration of the numbers of colonies of various species in a



FIGS. 112-113. An area on the campus of the University of the West Indies, Trinidad, that had a high concentration of nests of attines over a 5-year period. The sites of the nest of each genus is marked by its first letter (My for *Mycocepurus*). There were 12 large trees (the circles) down the center and the north boundary was marked by a *Dracanea* hedge (the xxxx region). The area studied was 18 × 77 meters and the south margin was shortened in



the diagram since no ants occurred there. See explanation in the text. (112) The location of the colonies in July, 1965. The five *Atta cephalotes* nests (AT) had just appeared in this month. (113). The location of the colonies in August 1968. The one remaining *Atta* colony moved from a position between trees 6 and 7 to the base of No. 1.





FIG. 114. The crescentic craters of six large *Sericomyrmex urichi* nests at the base of No. 11 tree in 1964. The location of M (*Myrmicocrypta buenzlii*), Myc (*Mycocepurus smithi*) and T (*Trachymyrmex urichi*) are also shown. The *Dracaena* hedge is in the upper left.

limited area (figs. 112–114). The numbers may seem exceptionally great, yet must be representative of the situation in much of tropical America and show the important role that these ants occupy in the general environment of tropical soils, plants, and animals. The campus may be considered to be representative of the highly cultivated flatlands and Trinidad has been intensively exploited by the western world since Columbus came in 1495. Other studies here have shown that the same species are abundant in cacao and coffee plantations. The average annual rainfall on the campus is 1,524–1,728 mm. (60–70 inches) and there is a December–April dry season. The census was taken in June–September at the time of the usual rainy season although in 1967 this was delayed and affected the visibility of the nests.

The area selected for the study was easily marked by a row of *Dracaena* plants that formed a dense hedge several meters high of straplike leaves which bordered the college tennis courts on the west. Next was a row of *Peltophorum pterocarpum*, yellow-flame trees from the Indo-Malayan region. In 1964 there were twelve in the row and then one died and was removed (No. 12). The trees cast dense shade over an area approximately 18 by 77 meters in area. Grass of the general campus entered the shaded area from the south. Because of the shade there was little grass and herb growth in this area except at the two ends where the rising and setting sun could strike.

In 1964 representative nests of the three most

common species were carefully excavated and the ants counted, as noted in this chapter. One of *Myrmicocrypta buenzlii* had some 1,700 workers (1,558 counted) distributed in three separate gardens. One of *Sericomyrmex urichi* had some 2,000 workers (1,691 counted) in seven gardens (fig. 89) and one of *Trachymyrmex urichi* had some 1,000 workers (763 counted) and an equal number of males and females in six gardens. The ants of the *Sericomyrmex* were particularly numerous at the base of No. 12 tree and seven craters showed clearly in one photograph. Sixteen nests of the *Trachymyrmex* were noted.

In 1965 a census of active colonies of the same area was undertaken and later continued. The results of the 1965, 1967, 1968, and 1970 censuses are shown in Table 2.

Differences in the census results may have several explanations in addition to the actual existence of more or fewer colonies. In 1965 the weather conditions were optimum, *Cyphomyrmex* was not included and the five *Atta* were new colonies from a mating flight of some two months earlier. In 1967 a prolonged dry season kept many colonies underground in an estivating condition; three of the *Atta* colonies had been removed and one of the two left had died out. It was estimated that only a fraction of the *Myrmicocrypta* (fig. 78) was found. In 1968 the weather was more normal and it must have been a time of extreme activity for the *Mycocepurus*; the one *Atta* colony had survived from 1965, yet it moved from between trees No. 6 and 7 to the base of No. 1 in response to excavating the center of it in 1967. It was poisoned just before my 1968 visit and no other colonies were present. There were signs of 18

TABLE 2

Species	Year			
	1965	1967	1968	1970
<i>Cyphomyrmex rimosus</i> Spinola	—	—	1	—
<i>Mycocepurus smithi</i> Forel	7	16	39	—
<i>Myrmicocrypta buenzlii</i> Borgmeier	60	16	67	6
<i>Sericomyrmex urichi</i> Forel	67	10	31	19
<i>Trachymyrmex cornetzi</i> Forel	—	—	4	1
<i>Trachymyrmex urichi</i> Forel	18	22	17	6
<i>Acromyrmex octospinosus</i> (Reich)	2	2	2	2
<i>Atta cephalotes</i> L.	5	1	1	—
Total	159	67	162	34

additional craters of *Sericomyrmex* in addition to the 31 active.

The 1970 census represents no more than a fraction of the colonies. There were 4 additional inactive nests of *Sericomyrmex* and other colonies of *Myrmicocrypta* and many of *Mycocepurus* were probably present. The explanation is that the rainy season came late (first week in June) and the ants likely brought in new substrate then. At the time of the census (June 25–26) the ants were probably working on the gardens underground. The surface of the area was littered with the fallen fruit and leaflets of the trees, rendering visibility of the craters poor.

The 81 square meters of area between trees 9 and 11 and the *Dracaena* hedge in 1968 had 51 craters of ants of 5 species, an average of 1 nest per 1.6 square meters. In a particularly crowded area, that between trees 10 and 11 and the hedge, there were 36 craters in 20.25 square meters or 1 nest per 0.56 square meter. Quite commonly here in past years, when *Sericomyrmex* had large, conspicuous crater entrances to their nests (fig. 114), there were entrances of the smaller species on the far larger craters. There was no hostility and the chambers of all were separate.

Over this five-year period it is clear that a large number of colonies of three species were present, with greatest concentration towards the west end of the area. Here they were so dense that workers must have foraged by one another without hostility and there was ample substrate for all. The greatest aggregate bulk of gardens probably belonged to the *Sericomyrmex*, a genus that has been largely ignored because of its nocturnalism and inconspicuousness.

Great stability of the colonies was shown in the 1965–1970 period by one of the *Acromyrmex*, which stayed in the same place, and some of the *Sericomyrmex* and *Trachymyrmex*. A colony age of at least five years is suggested by this evidence.

Other large-bodied *Atta* females from a colony often descend from their nuptial flight in the same general area. Autuori mapped the sites from such a flight of *sexdens* in Brazil and the resulting young. He accounted for the failure of most of the new colonies on the basis of mortality of the queens in the first months of independent life. The females of *Atta colombica tonsipes* descended close together on the golf course at Summit in the Panama Canal Zone in one year. They probably originated from mature colonies in the adjacent woods of a

ravine (fig. 52). An area of 232 square meters near here in 1971 had 70 young colonies.

#### *Colonies of an Acromyrmex*

The numbers of nests of *Acromyrmex* (*Moel-lerius*) *landolti*, originally named as *balzani* subspecies *myersi* (Weber, 1937), were determined in three areas on the Rupununi Savannas, in Guyana (Lat. 3°28' N., Long. 59°42' W.) in July, 1970, by Peter Weber. The plots were 50 feet on a side (15.24 meters) and the area of each was 232.3 square meters. The region is tributary to the Manari River which drains by way of Rio Branco to the Amazon system and is part of the interior grasslands of South America. The ants harvested *Trachypogon plumosus*, *Andropogon*, *Axonopus* and other grasses. Termites, including *Amitermes* with nests up to three meters high, and *Atta laevigata* are the other animals important here in cutting the grass and woody vegetation. The census areas were marked off with a tape measure and were typical gentle grassy slopes; no *Amitermes* or *Atta* nests were present (fig. 83).

Each nest was of a separate colony and clearly marked by a crater. It was a period of maximum ant activity during the height of the rainy season. An average nest was estimated to have five gardens of a total volume of 500 ml. and a weight of some 33 grams.

Census areas A and B each had 18 nests and C had 23 nests (fig. 115). The site of each nest probably represents the approximate spot where a female descended to the ground after her nuptial flight. These ants were clearly the dominant animal in the ecology of these areas.

#### EMIGRATIONS OF COLONIES

It sometimes happens that a nest may be exposed suddenly to an unfavorable environmental change, such as structural damage or flooding. Other animals, too, will move their brood out of the way but these ants have also to break up their delicate fungus garden and move it piece by piece. There are ample opportunities in the process for alien fungi, bacteria and small animals to invade the fragments and cause harm to the ant fugus.

A response to mechanical damage was shown by an *Acromyrmex histrix* nest in the Orinoco delta, Venezuela (Weber, 1947). The nest was two meters above soil level and suspended in humus between two palm trunks. The fungus



garden was removed to a large leaf on the ground and spontaneously broke into small fragments. The ants gathered these fragments by the following morning and moved them to a new site above the former. They had reconstituted a new garden of the original size within 24 hours of the damage. During this time the humidity was constantly high and desiccation was not a problem. The fungus was growing all the while and had much to do with binding the fragments together.

A *Trachymyrmex isthmicus* colony in Panama moved its nest under no known stimulus unless it was waterlogged clay soil from heavy rains (Weber, 1941). A file of the ants was encountered at 10:50 A.M. in which each ant going in one direction was carrying a piece of fungus-coated substrate, one of the brood or even a fragment of fresh insect feces during 65 continuous minutes of watching. Those going in the reverse direction had no loads. All were marching between two holes separated by 37 cm. in a direct line. They were, however, following an invisible path over two large roots, a number of fallen leaves and the crater of their old home so that the route as taken was 52 cm. All ants did not follow the invisible path exactly but the deviations were a fraction of a centimeter. When one worker would deviate slightly, the next would sometimes but not always follow the deviation. It would appear that the ants were not only following a scent trail but may have used their eyes to detect landmarks. When a number of ants passed over a trail, a strong enough odor was laid down so that other ants followed without difficulty. The studies in much later years by Moser and others have shown how this scent trail is laid down. The awkwardness of the load caused minor deviations as the ants walked over the irregular surfaces. There was an average of 2.2 laden workers per minute on the trail at several times. Seven ants were carrying loads to the new nest site and 14 were returning empty to the old site in one 10-minute period during the afternoon. The 52 cm. path was traversed by laden ants on the average in 68 seconds at one time and 69 seconds in another period. The return speed of four unladen ants was an average of 57 seconds, the ants speeding up noticeably when they crossed over a smooth dead leaf.

The ants were engaged in moving all of that day. A rain at night stopped this activity. The following morning the area was deserted

and the craters beaten down; 60 mm. of rain fell in the afternoon and erased all signs of the old and new crater entrances. There was limited moving of material from the old site on the third day but the bulk of the nest had evidently been moved.

It appeared that heavy rains may well have caused the moving. During the week ending two days before the discovery, 210 mm. of rain fell and must have soaked the site. The moving probably started the day before the ants were seen. Three days were probably consumed in moving and the number of trips necessary was probably of the order of magnitude of 10,000.

Less detailed records are available for other attines that moved their nests. One of the best is an *Atta cephalotes* (the two-year colony above described) that moved its nest from an original site under one tree to another at the end of the row, as a result of excavation of part of the nest.

#### HIBERNATION

Hibernation, if the term can be applied to animals such as these, is a cessation of activity in response to low temperature. The response might also be termed torpidity.

#### *Hibernation in Trachymyrmex septentrionalis*

This northernmost species becomes hard to find at its northern limit in late August, most activity above ground ceasing except in midday or after warm rains. There is little or no excavation and the summer craters become washed or blown away. Few workers are found above ground in September.

The ants go into hibernation in New Jersey in September or October according to the weather.

The autumn of 1962 was warm, and on October 6, a few craters could still be found. The temperatures under them at 10 cm. were 19.4° C, at 20 cm., 18.2° and at 30 cm. 17.8°. Ants were found under one crater at a depth of 12 cm., under the second nest at 11.5–14 cm. and under the third at 9–11 cm. Only the latter had an obvious garden and this was very small. In previous years ants were found in the fall with tiny masses of dark brown substrate with withered hyphae.

New Jersey laboratory colonies, when kept at the same latitude in Pennsylvania, show a partial hibernation that appears to be a response



to the season rather than to temperatures. The gardens gradually became smaller in October and reached their smallest size in December and January. This is true whether temperatures are in the 18–26° C range or whether they are kept constant at 26–27° C. The gardens increase in size during late January and February.

The gradual warming of the subsurface sand in April usually brings the ants out of hibernation in New Jersey. Temperatures in April over a number of years were taken at the same site at 10 cm. intervals to a depth of 40–50 cm. The area was one that had numerous colonies every year. Since April is a month with highly variable temperatures, the records vary in contrast to those of the tropics. If the ants do not emerge in April, they appear in May.

Its seasonal activity starts in the spring and I have noted its emergence at a particular site (Lat. 39°40' N.) in the Pine Barrens during 1947–1969 as follows:

April 23 appeared to be the earliest (1954), followed by April 25 (1957 and 1960). Other early dates were May 5 (1959 and 1963), followed by mid-May (1947, 1958, and 1965–1967). The latest was estimated to be in 1968 when eggs only were present on June 13 and the ants probably emerged about June 1. Generally in the spring it is necessary to have temperatures of 18° C or higher, at depths of 20 to 30 cm., for several days before the ants can warm sufficiently to crawl to the surface. The surface will then be warmer and the ants will respond by greater activity.

Workers of this species in nature in Florida could crawl about sluggishly when unearthed from their nest at 13.4° C. They were previously clustered together in torpor. In general the species was not an active forager here until the soil surface warmed to 18–22° C or more. Refrigerated colonies, including the males and females from New Jersey, could crawl about actively at 13° C. At 0° C they became motionless and fell on their sides but some would recover after a month of this temperature.

#### *Reactions of Other Ants to Low Temperature*

One record is of the yeast-culturer, *Cyphomyrmex rimosus*, in Florida. The coldest weather came in 1954 with frost (0° C) on December 21. It was so cold on December 2–26 that these ants almost disappeared temporarily from their known nesting sites; temperatures at 2.5 cm. and at 5 cm. in the soil were 18.0° and 18.5° C, respectively, in mid-afternoon. Several workers were seen to carry others from these depths. This appeared to be the lower limit of activity for this species.

Cold tolerance of species near their most southern extent in Argentina (34° 30' S. Lat.) is shown by the following observations of ants outdoors.

The lowest temperature at which *Acromyrmex lundii* ants were active was 8.7° C; a few continued to return slowly from midday foraging when the temperature was 9–11° C later in the day. Workers of *Acromyrmex ambiguus* moved normally at 11.5° C and attacked when they were disturbed. Both species cut *Pelargonium* flowers at 12.0° C. The *lundii* workers slowly carried exhausted substrate out of the nest at 12.3° C. *Apterostigma steigeri* workers walked slowly at 15.8° and were seen to forage at 17.5° C.

Freezing surface temperatures are encountered at both extremities of the range of *Atta* but rarely in the south. The ants retire to the fungus chambers of the nest at the approach of cold weather, where freezing temperatures are seldom if ever encountered in the north and probably never in the south. It may be said, therefore, that the ants themselves are never actually exposed to freezing temperatures. Workers of *vollenweideri* were exposed briefly to 10° C and were not harmed. Dormancy cavities with torpid ants or waste material were described in the *texana* winter nest (Moser, 1963).

At both extremities of the range the nests occupy sunny sites. This is clearly useful in temperate regions, permitting more hours of daily activity on sun-warmed soil than would be the case in shaded areas. Both occupy compact soil although the northern species is often found in sandy areas.

## 7. FORAGING BEHAVIOR

The activities of the ants in finding the substrate, usually leaves, are discussed here. This foraging behavior in the leaf-cutters may produce dense, spectacular files of the workers that first impress the visitor to the tropics.

### TRAILS

#### CHEMICAL TRAILS

A trail-marking substance or pheromone laid down by *Atta texana* and produced by the poison gland is deposited by the sting (Moser and Blum, 1963). When a source of leaves was discovered by a laboratory colony, the ants making the discovery touched their gasters regularly to the ground at 2 or 3 mm. intervals while returning to the nest and thus laid a trail of scent. The first ants did not return to the nest with leaves. The substance is a clear, viscous liquid, soluble in methylene chloride and carbon tetrachloride, recently identified by Moser (1971) as methyl 4-methylpyrrhole-2-carboxylate. When a poison sac is crushed on a glass slide this liquid quickly solidifies into a hard, shiny amorphous material resembling clear fingernail polish. At least two components, one volatile and the other non-volatile, were later found to be present (Moser and Silverstein, 1967). These and other pheromones were reviewed by Moser (1970).

#### PHYSICAL TRAILS

The making of physical trails is a conspicuous feature in *Acromyrmex* and *Atta* (figs. 2, 116-119). They become worn by constant use and are obvious to the human eye. These lead to and from areas of substrate-gathering. The smaller ants of more primitive genera may show stages leading to this behavior of the highest attines (Weber, 1958). The workers of *Cyphomyrmex rimosus* in Florida were observed occasionally to follow the paths of one another. Another kind of trail-making, without the cleared aspect, is described in chapter 6 in the section on *Trachymyrmex isthmicus*.

The workers of *Sericomyrmex urichi* in Trinidad formed short, densely traveled trails in the immediate vicinity of the large craters but only at night. These become somewhat cleared of debris towards the nest entrance. Workers of

*Trachymyrmex urichi* here also formed similar trails at night but of narrower dimensions, and occasionally followed one another in daytime foraging.

The trails made by *Acromyrmex octospinosus*, *lundi*, and other species of the genus are well-defined physical structures as in *Atta*. They differ from *Atta* in having narrow trails, only 1 or 2 cm. wide in most cases, while in *Atta* a trail may be 30 cm. wide (fig. 118). Commonly the trails are sunken and in grassy areas the grass may grow over the edges so that the trails may be largely overlooked. The trails themselves are free of grass or leaves. In *lundi* and other species of the Argentine pampas as many as eight trails may radiate out in all directions from the nest (fig. 117). Other species in tropical rain forest may show little or no trail-forming on the forest floor.

A thriving colony of *octospinosus* in Trinidad in 1964 had its hidden nest along the weedy railway right-of-way in St. Augustine. This was protected by a barbed-wire fence, which was of advantage to the ants since humans could not easily get at them. From this sanctuary the ants foraged onto the well-kept grounds of the University of the West Indies. Their oldest path was sunken from long use and for most of its length it was superficially invisible under the closely cropped lawn. Upon reaching an area of citrus, cashew, and other trees, the ants spread out and did not form distinctive paths in the shade under the trees.

One resourceful colony of the same species was nesting in the Trinidad Botanical Gardens in the crown of a large palm. In this case it must have been disconcerting to the gardeners to see the long files of ants marching up the tree with their burdens of leaves, instead of down.

The subject of trail-formation is an interesting one and the genus *Acromyrmex* may be commended to anyone interested in the development of this trait.

This development may also be followed in a colony of *Atta*. Five colonies in Trinidad of *Atta cephalotes* less than two months old started to make rudimentary trails within a fortnight of their emergence to the surface. At first ants tended to follow one another in all directions from



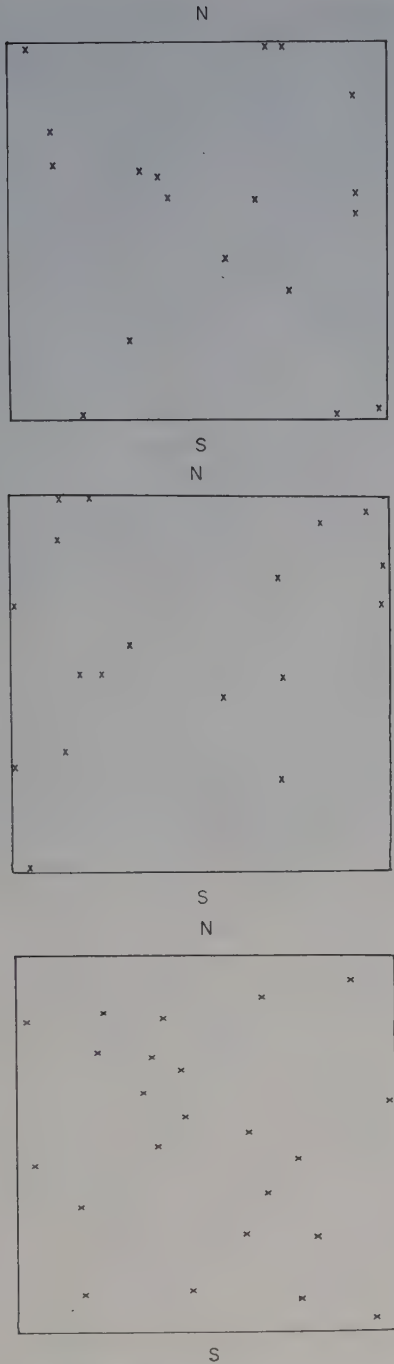


FIG. 115. Census areas *a-c*, each 50 feet (15.24 m.) on a side, showing the location of nests of *Acromyrmex* (*Moellerius*) *landolti* (*balzani*) on the Rupununi Savannahs, Guyana (after Peter Weber). The ants harvest *Trachypogon plumosus* and other grasses for substrate and are the chief agent, with termites such as *Amitermes* and the ant *Atta laevigata*, in harvesting the savannah plants. Areas *A* and *B* had each 18 nests and area *C* had 23 nests.



FIG. 116. Trail made by *Atta cephalotes* near the engineering plant of the University of the West Indies, Trinidad. The ants cut and removed the closely mowed savannah grass to make the trail.

the entrance to the nest as they foraged within a few centimeters of the crater. Not all colonies developed trails at the same rate. The most noteworthy one formed a trail 320 cm. long after some two months of colony development. The workers, which were still of the small to medium sizes, followed the same route with great consistency as in *Trachymyrmex* above. The trails were partially cleared of fallen vegetation and clear to the human eye.

Like the grasslands-inhabiting *Acromyrmex*, *Atta sexdens piriventris* in south Brazil, in a similar habitat, had numerous narrow trails radiating out in different directions, while the tropical *cephalotes* and other species tend to concentrate on fewer but broader trails.

The trails of *Atta* in the course of long use may become so distinct that considerable conscious effort may be imputed to the ants (fig. 116, 118). They do not, however, appear to cooperate at any one instant in clearing a path of debris but





FIG. 117. Eight trails radiating from a thatch mound nest of *Acromyrmex ambiguus* on the Argentine pampas. The maximum diameter of the mound was 122 cm.

rather an ant or two sporadically may remove a leaf or fallen twig from the way. Even more commonly the ants may cut it up in pieces and take it to the nest as substrate. A tin-foil wrapper falling upon a trail may have sections cut out in that part lying on the trail so that the ants may resume their progress. Since many thousands of trips are made over a given point in a mature trail, random actions of this type are sufficient gradually to clear a path.



FIG. 118. Trail made by *Atta cephalotes* in Trinidad. Parts were 30 cm. wide.

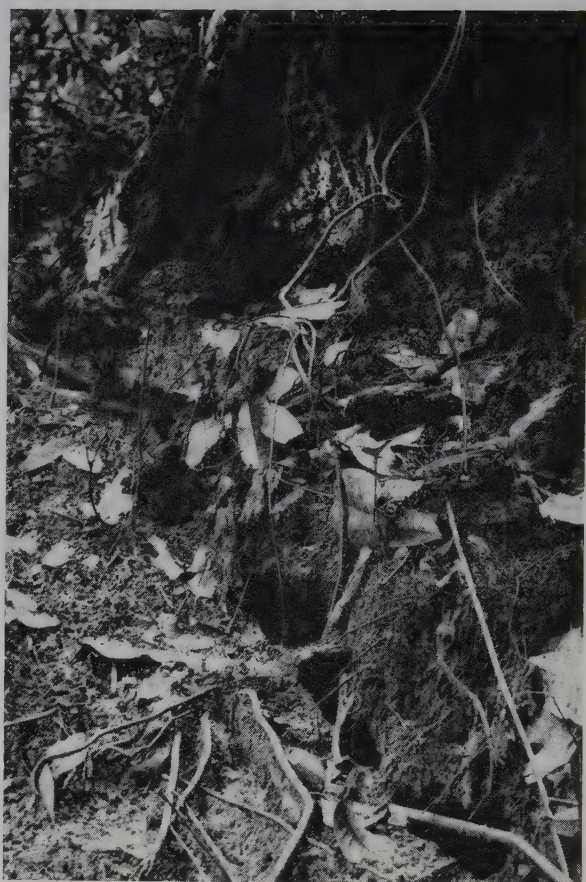


FIG. 119. Sunken trail made by *Atta cephalotes* in going down the side of a ridge in Guyana rain forest.

An unusually broad and well-defined path of a *cephalotes* nest in the Trinidad rainy season of July, 1964, was kept clean partly in a different manner (fig. 118). The path led through a grassy glade between trees and was as bare and flat as any human trail. The ants must long ago have cut the grass in the way but dead leaves and twigs were continually falling on the path. At times of a heavy rain this section of the path was flooded and the water tended to wash the debris to the side.

Trails passing up or down a slope may gradually become eroded as trenches or even tunnels (fig. 119). Here again, if the ants sporadically but persistently remove fallen debris, a heavy rainfall will aid the process of clearing the trail and deepening it.

It seems unnecessary in the above cases to have a continuous trail of scent. When it is washed away the ants may follow the trail anyway. Possibly a worn trail could serve as a



physical stimulus in itself. How much of a part memory plays in this is unknown. These clear-cut trails have such a daily traffic that if memory is possible it need only be of a few hours' duration.

#### CYCLE OF FORAGING

The foraging behavior and trails of a colony of *Atta cephalotes* in Guyana were determined by Cherrett (1968). It had four principal entrances and five refuse piles. It was estimated to be about one year old but may have been closer to two years. The superficial part of the nest occupied 56 square meters. There were at the time six principal trails which had a total length of 8,287 meters (9,063 yards), or over five miles. Cherrett made hourly counts of activity on the trails, correlated with temperature, relative humidity, and light intensity. The ants were primarily nocturnal. One *Cassia* tree was attacked on 19 consecutive nights and 25 per cent of 122 different plants were cut on more than one occasion. Of a total of nine trails, three never carried more than 3 per cent of the incoming laden ants. The total number of incoming ants varied from 2 to 359 in three-minute periods. The ants traveled as far as 65 meters from the nest to cut but the mean distance in one series was 47 meters. Of 72 species of woody plants identified in the nest area, 36 were attacked.

#### NUMBERS OF ATTAS ON TRAILS

The numbers of attines on trails varies from zero to a confusing impression of a moving river of ants. A large trail with maximum activity shows so many ants moving past a given point that counting is difficult. To add to the confusion the ants are moving in both directions, some concealed under their burdens, and occasionally one will suddenly reverse course.

Numbers of ants on a typical active and shaded trail of *Atta cephalotes* in Trinidad were counted at three points. One point (A) was on the trunk of a cacao tree that was being defoliated by the ants. A second point (B) was near the base of this tree where other ants were converging and the third (C) was farther along the main trail.

From 9:10 to 9:20 A.M. (temperature 27.3° C) the following ants passed with leaves: A-160 ants; B-578 ants; C-564 ants.

Soon a short, hard rain fell and many ants

dropped their loads. As soon as the rain stopped, counting was resumed of those ants carrying leaf sections towards the nest.

In four minutes the results were: A-12 ants; B-52 ants; C-61 ants.

It was clear that the rain had caused most of the ants in the tree to stop cutting leaves and the numbers at stations B and C reflected those en route during the rain that did not drop their loads.

At this time a two-minute count was made of those ants moving away from the nest towards the various cacao trees. They were of course not carrying substrate: A-26 ants; B-128 ants; C-134 ants.

This particular colony had a number of such trails and the ants were climbing a number of cacao trees; it would be considered a time of maximum activity. The figures show that a sudden shower is a mere temporary interruption and that some of the ants remain at work up in the crown of the tree. Immediately after the rain passes the trails swell with outgoing ants.

#### DAILY CYCLE OF FORAGING

The long files of leaf-cutting ants returning to their nests have excited the interest of people in the tropics, second only to their effectiveness in defoliating plants. Numerous observers have noted the files of ants carrying leaf sections during the day, since this coincides generally with human activity in these regions. Other observers have noted their nocturnal activity, and over-night defoliation of plants is well known to the residents.

Aspects of their diurnal activity in the Panama *Atta* have been measured by Parker (1925), Lutz (1949), and Hodgson (1955). Goetsch (1939), following the line of Santschi's North African studies on desert ants, also found a light compass orientation on the diurnal trails. This emphasis on diurnal activity naturally concentrated on the cyclic activity that culminated in leaf-gathering, and tended to ignore the internal factors in the fungus gardens. The discarding of refuse noted by Hodgson was probably an indication of the constant reworking of the garden; the refuse was probably old and exhausted substrate. One of my students, David Klingener, took pains to compare his studies with those of Lutz at the same Panama Canal site. Lutz's conclusions were:

1. The leaf-cutting activity under rain-forest conditions seems to be strictly diurnal, with initiation of work at daylight and cessation at nightfall.
2. Leaf-carrying ants travel on the average 1 meter in 36 seconds on the trail or 40 seconds if the ants were intercepted by unladen ants.
3. The burden of the leaf seems to stimulate the carrier to go nestward; its absence stimulates movement in the opposite direction.
4. There is a positive correlation between the weight of the ant and its burden-carrying efficiency (weight of burden  $\times$  speed).

Klingener in general obtained results similar to points 1-3 above but was aware that *Atta* often is nocturnal. He did not feel that there was a chemical polarity to the trail, coming to this conclusion by reversing pieces of fallen wood over which the ants were traveling. Light was felt to be an uncertain factor because of changing values over the trails and he concluded that orientation involved a complex of factors.

Hodgson measured the *Atta cephalotes isthmicola* foraging pattern over a July 14-August 7 period, during which the pattern was disturbed by rain on all but four days. The diurnal pattern of activities, once initiated, appeared to bear no relation to the fluctuation of light intensity, temperature, or humidity and stopped at about the same time. Rain caused the ants to return to the nest, later to resume foraging. The smallest workers came to the exit holes prior to foraging when the first light fell on these holes. This light intensity was about 0.3 foot candle. The smallest workers in turn may have excited the leaf-cutters to start out on the forage trails. Marking experiments showed that the same workers may participate in foraging and detritus removal. The unladen workers no longer left the nest when the light intensity dropped below about 3 foot candles and those on the trails already unladen started to return. Detritus removal was carried on throughout the 24 hours of two days. The pattern of foraging was determined first by the temporary indistinctness of part of the odor trail before it was strengthened by the passage of many ants, second by a gradual afternoon decline of laden and unladen ants on the trail, and third by the evening decrease in illumination which results in

an increase of ingoing workers and a decrease in those leaving the nest.

Studies of five young *Atta* colonies (chapter 6) in Trinidad in their first few weeks of above-ground activity showed early stages in rhythmicity of foraging and in closure of the nest entrance (Weber, 1966b) (fig. 112).

Foraging usually was initiated with increasing daylight. This was perceived by the ants through the plug of loosely curled and dry leaflets from the trees overhead that had been placed by them in the nest entrance the previous late afternoon. The nest most easterly of the five received direct sunlight by about 6:40 A.M. when the sun was 10° in the sky. The ants then clustered about the opening and in one case carried out exhausted substrate five minutes after the sun struck.

The ants foraged lightly all day, rains permitting, and would close their entrance at a variable time in the late afternoon, often by 4 P.M. and regularly by 6 P.M. On a sunny day with much foraging they usually ceased about 5 P.M. Exceptionally a young colony would forage at night, as did one at 8 P.M. on a clear and extremely humid night following 50 mm. of rain on the previous 1½ days. The opening of the nest would be delayed if rain fell in the early morning. During the day a heavy rain would cause foraging to cease. A light shower, attended by raindrops sprinkling down from the leaf canopy, would not cause a cessation of foraging. An afternoon rain would cause the ants to close their entrance early.

The large colonies of *cephalotes* foraging far from the nest by late afternoon will often be returning during the early part of the night. Workers may not then be leaving the nest and the result is that activity ceases during the night, not to resume until dawn.

#### *Foraging by Other Attines*

The small attines also may be nocturnal as well as diurnal. Foraging is not a conspicuous activity when the ants are slowly and singly moving about.

Colonies of *Mycetophylax conformis* nesting in seashore sand of Trinidad and ordinarily nesting within a few centimeters of the grass that they used for substrate, in one example must have had to travel a minimum distance of 350 cm. to the nearest site for the grass they had to use.

The genus *Apterostigma* has been considered



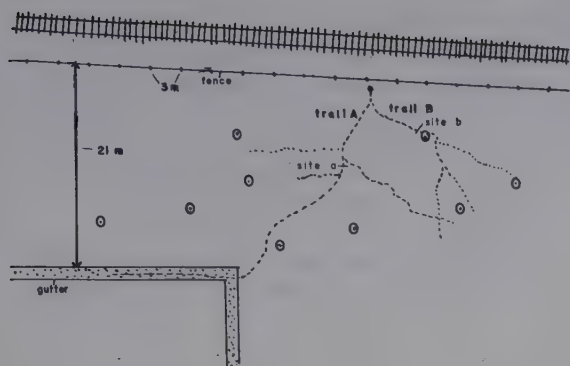


FIG. 120. An active colony of *Acromyrmex octospinosus* in Trinidad that consisted of an estimated 5,900 foraging workers. The ants nested at the edge of a railroad right of way and foraged on the grounds of the University of the West Indies. The main trail forked (A and B) and counts of the foragers were made at two sites (a and b) on these. Trail A was approximately 50 meters long, terminating at the concrete gutter at the side of a building. The circles indicate trees that in some cases were being defoliated. Counts were made for 15 minutes each at 4-hour intervals throughout the 24 hours. The numbers were correlated with the condition of the sky and precipitation.

typical of the tropics yet the species *steigeri* was active occasionally in the winter in suburban Buenos Aires. On May 21 one was slowly carrying substrate over a 16° C soil surface and on August 26 a worker appeared briefly at 15° C.

Colonies of both *Sericomyrmex urichi* and *Trachymyrmex urichi* foraged slowly in the early night in Trinidad, as noted earlier under trail activity (p. 72).

#### FORAGING BY ACROMYRMEX

Foraging by the species of *Acromyrmex* is much like that of *Atta* and they are active over an even greater range of habitats and temperatures. *A. hispidus* and *lobicornis* from Santa Fe Province, Argentina, were kept experimentally in Buenos Aires. When exposed to temperatures of 13–15° C their foraging reactions were similar to those of *lundi*. When exposed in a 10° C breeze for photographing, they were no more sluggish than *lundi* and survived the brief exposure. *Acromyrmex discigera* of south Brazil was reported by Moeller to show full foraging activity at 12° C.

#### Year-round Activity of *Acromyrmex lundi*

In contrast to the highly restricted seasonal activity of the northern *Trachymyrmex septentrionalis*, the southern *Acromyrmex lundi* showed

the following year-round activity (Lat. 34–35° S.) in 1960–1962:

Winter—A few ants foraged during June and July when the temperature was above 12° C. Generally they went out from the nest when it was warmer than this but when the temperature started to drop to 12° C they slowly returned. The ants actively harvested leaves at 15° C. Many ants that were found dead or dying on June 24–25 may have been affected by the

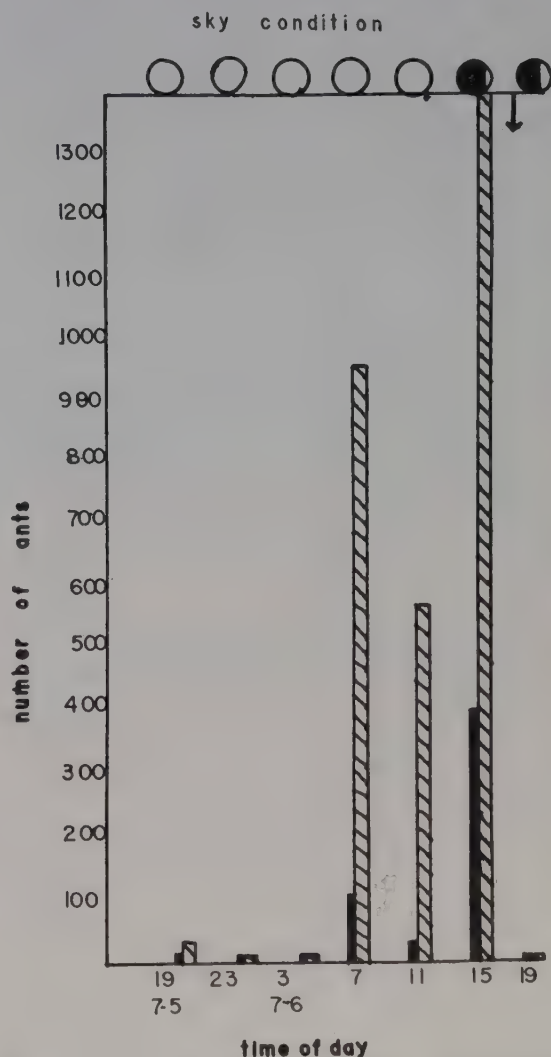


FIG. 121. The ants active in a 24-hour period starting with 7 p.m. The sky was clear until between 3 and 6 p.m. of the following day. At 3 p.m. about 1,400 ants were active on the two trails. The black vertical bar indicates the number of ants carrying leaves, the hatched bar indicates the total with and without loads.

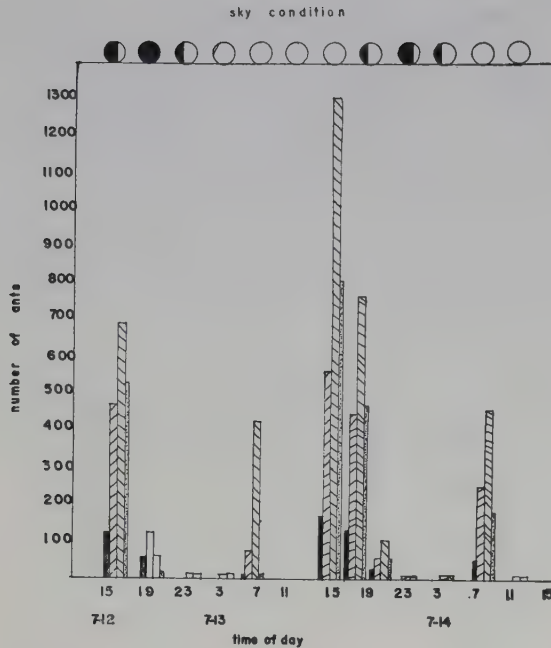


FIG. 122. The foragers in a 48-hour period starting with 3 P.M. The vertical black bar indicates ants carrying leaves at site *a*, the dotted bar indicates the ants carrying leaves at site *b* and the hatched bars indicate total ants with and without loads at the two sites. The fewest ants were active at 3 A.M. and 11 A.M. 1,300 ants were present at site *b* after 16 hours of clear skies at 3 P.M.

unusual cold (minimum  $-2^{\circ}\text{C}$ ) of the previous week.

Spring—The activity increased to normal during August and September, winter conditions ending in the former month. August marked the month with least leaf covering for vegetation and the ants then harvested leaves which they did not ordinarily attack, for example cedar. The ants formed slow-moving files at  $10\text{--}12^{\circ}\text{C}$ .

Summer—Full activity. By February 10 the ants were foraging more at night than in the day in order to avoid the heat and dryness, harvesting the imported succulent, *Aloe arbore-scens*, perhaps for added moisture for the garden. They engaged in maximum trail-making by this date.

The fact that at the threshold of lethal temperature all ants do not die was illustrated strikingly with refrigerated *Acromyrmex lundii*. An estimated 1,000 *A. lundii* were placed in 7 test tubes with some of their garden and brood and stored in a refrigerator which was kept at  $4.5$  to  $8^{\circ}\text{C}$  for 17 days. After 5 days at  $5\text{--}8^{\circ}\text{C}$  both the ant fungus and the ants were normal

and could revive quickly. Lethal conditions were reached after 12 more days. Three ants survived, one of which could move only single joints while the other 2 could walk feebly. A larva could still move its mouthparts and head capsule. The infesting nematode worms remained viable while the ant fungus became overwhelmed by a *Mucor* type.

These outdoor and refrigerator records appear to be the only specific records in the gardening ants of the important limiting environmental factor of cold. They suggest that the fungus can withstand lower temperatures than the ants, as does more limited evidence in the case of *Trachymyrmex septentrionalis* in the north.

#### Foraging Cycle in *Acromyrmex octospinosus*

Several 24-hour cycles of *Acromyrmex octospinosus* were followed by my students Peter Delmonte and Stephen Hitchner (Weber, 1966b). Colonies were chosen that foraged regularly on well-defined trails in savannah grass and they also crossed shallow concrete water drains (figs. 120–124). Mostly they gathered leaves of cultivated bushes and trees. Determinations of activity for 15 minutes each at 4-hour intervals (3, 7 and 11 A.M.; 3, 7 and 11 P.M.) were made throughout the day and night. It was a typical rainy season period in July, 1965. The relative numbers of ants passing fixed points with and without leaves were determined. Rain caused foraging to cease. Rain on one day at 11 A.M. caused them to cease foraging until 5 P.M. Their numbers on that date, as they went out on the trails and returned with leaves, increased into the night, dropping off markedly after 3 A.M. In one cycle of 48 hours, the peaks of foraging and trail activity came after more than 12 hours of clear sky with maximum activity at 3 P.M. and almost none at 11 P.M. and at 3 A.M. Although most of their foraging was done in the daytime, they appeared to be equally efficient in foraging at night. However, efficiency decreased by early morning, the coolest time of the 24 hours (about  $22^{\circ}\text{C}$ ). They avoided open areas in the sun when the surface was  $38^{\circ}\text{C}$  at one spot on the trail.

The substrate each ant carried had an average weight of 7 to 9 mg. in 300 samples. The average weight in another sample of 72 was 19 mg. The latter was of mostly broad-leaved plants, the former included grass leaves. The average speed of ants carrying loads was 29



seconds per meter (21 ants). The ants were much slower when going through grass. Ants without loads traveled a meter in 13 to 19 seconds. The charts (figs. 121-124) show their numbers and activity with respect to time of day, sky conditions, and temperature.

#### CUTTING OF VEGETATION

Leaf-cutting has been a matter of much popular interest. The ants attack a leaf relentlessly and may cut much of it up before moving on (figs. 125, 127, 128). The ant works from the margin, taking a firm stance by attaching the claws of the legs to the leaf. It faces inward and proceeds to cut an arc, using the body as the radius and turning. The base of the gaster or of the hind legs tend to be largely fixed points. The size of the section cut by *Acromyrmex* and *Atta* therefore tends to vary with the size of the ant. Then the mandibles are applied to opposite sides and they start a cutting action, alternately closing one mandible and the other. In an experiment in a sound-proof box at the Carnegie Institution of Washington, with the sound greatly magnified electronically, this was recorded as a rasping noise comparable to tearing a piece of cloth.

The speed of cutting depends on the nature of the leaf and the size of the mandibles. Flowers (modified leaves) are cut fastest. Among my numerous colonies of leaf-cutters, *Acromyrmex*

FIGS. 123-124. A small colony of *Acromyrmex octospinosus* in Trinidad that consisted of an estimated 900 foraging workers. The ants nested at the edge of a railroad right of way and foraged over one main trail to a clump of *Bauhinia* some 10 meters distant. The ants active on the trail are correlated with the condition of the sky and with the ground temperature of the trail. Rainfall is shown by arrows descending from the circles that denote the condition of the sky. The vertical black bar indicates ants carrying leaves and the hatched bar shows the total without substrate. Where two bars represent the temperature, the higher is that in the sun, the lower is for that in the shade. (123) A 24-hour cycle starting with 7 P.M. on one day and terminating at 7 P.M. the next day. Counts were made for 15 minutes each at 4-hour intervals. Ants were active on the trail all night long under clear skies. A shower at 11 A.M. did not interrupt them but a rain about 4 P.M. caused a cessation of activity. (124) A 48-hour cycle starting at 7 P.M. on one day and terminating at 7 P.M. on the second day. Few ants were active the first night under cloudy skies, then showers starting at about 6 A.M. and a rain at 11 A.M. kept activity down until 7 P.M. The ants maintained a high level of activity that second night. Rain after 11 A.M. again caused the ants to remain in the nest.

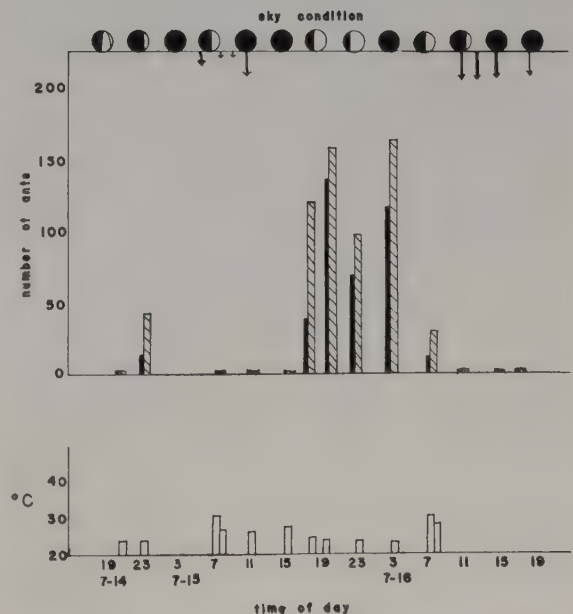
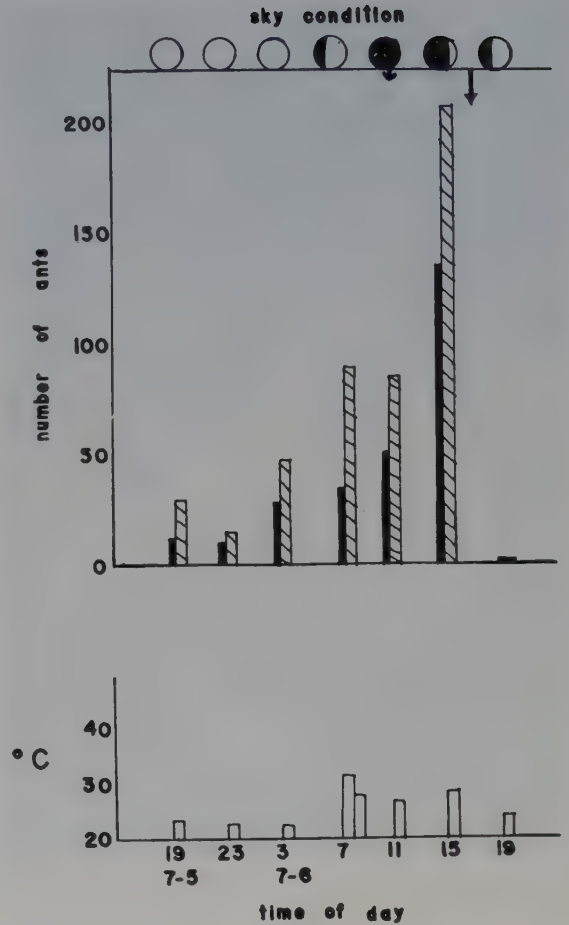




FIG. 125. Workers of *Atta cephalotes* cutting fresh leaves in the laboratory. The mid-ribs are left to the last.

*octospinosus* often out-performs *Atta cephalotes*, in part because their mandibles are more massive and partly because more of the larger-sized ants are cutting (fig. 126).

In a series of experiments with the fresh pith of grapefruit rinds having the oily outer cortex removed, the rate of cutting 20 grams was determined for different species and colony sizes. Colonies of both the above species with gardens of comparable size (5,000–7,000 ml.) cut about 3 grams of pith per hour at the fastest. The small media workers of both species cut this substrate along with much larger media and maxima workers. The weight of the pieces was comparable to fresh leaf sections.

Commonly the ants leave the mid-rib of the leaf if it is large. Every part of fresh rose flowers, however, is taken down to the last bit of the fibrous receptacle. They will also cut sections of ash-leaf petioles of two or three centimeters length and place these on the garden.

The size of the section cut out of a flower petal or a leaf cut by workers of smaller genera depends on the genus of ant. *Trachymyrmex* and *Sericomyrmex* cut sections only one or two millimeters in diameter.

The workers of these two genera also pick up small particles of substrate of a millimeter or two in diameter and plant them directly on the garden. Insect feces and woody particles are used by these and still smaller genera. Their gardens commonly are sprinkled with pieces of the carcasses of insects and these acquire growths of the ant fungus. Recognizable carcasses of arboreal ants in the attine gardens indicate that the ants pick them from the forest floor where they have fallen.

Insect feces particularly used are those of wood-boring beetles and of caterpillars. The latter contain still recognizable pieces of leaves and the ants may separate the pieces and plant them on the garden.

All of the species lick the pieces thoroughly, whatever the substrate, and often defecate on them before planting them on the garden as mentioned in chapter 6.



FIG. 126. Ants of *Acromyrmex octospinosus* cutting the fruit of a fallen papaya in Trinidad. Leaf-cutting ants scavenge for fallen fruit and starchy food in all urbanized areas within their range.



LEAF-CUTTING OF ATTA AND  
ACROMYRMEX COMPARED

The *Atta* colony is much larger than that of *Acromyrmex*, as are the largest workers. The files are bigger and more conspicuous. Nevertheless, the leaf-cutting activities are closely similar and, when a colony concentrates on one particular tree or shrub, the damage is comparable.

Both tend to have spurts of activity when they cut great quantities of leaves. Such spurts may come after a period of unfavorable weather such as rains (see above). The large quantities then may be carried into the nest much faster than the ants remaining here can cut them into very small pieces that are ready for the garden. The incoming ants at such times dump them at the base of the garden and return for more.

## SPEED OF ANTS CARRYING LOADS

The speed of *Acromyrmex lundii* workers carrying leaf sections over a level stone surface in the shade was determined during an early spring day (September 5) in Buenos Aires, Argentina. It was a time of representative maximum activity. The temperature of the stone surface at the start of measurements (3:13 P.M.) was 16.7° C, and dropped gradually to 16.0° C at the conclusion (4:33 P.M.). Corresponding temperatures at a height of five centimeters above the trail were 17.6 to 16.7° C, respectively. The route studied was one meter long, part of a trail of about 20 meters in length. There was an intermittent breeze that caused the ants with

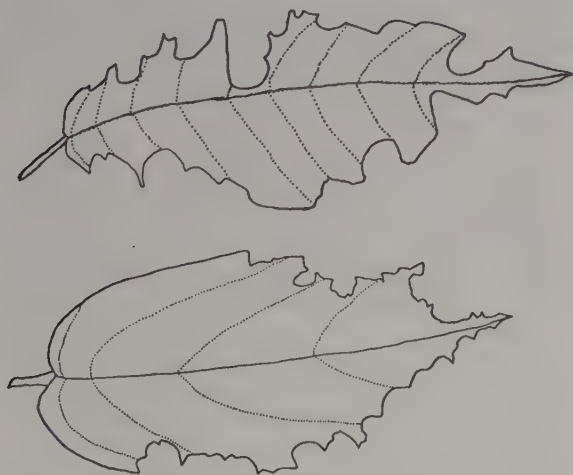


FIG. 127. Leaves cut by *Atta cephalotes*.



FIG. 128. Worker of *Atta texana* carrying a leaf section in the usual position assumed by the leaf-cutters with their burdens.

the larger loads to be momentarily stopped, and in one case an ant was blown over.

The time taken by 15 ants of various sizes was 50 to 212 seconds, the latter interval being required by a small ant with a large load during a breeze. The next longest time was 155 seconds and 3 additional ants took over 100 seconds. Eight ants took 51–85 seconds. The average of the 15 was 99 seconds which was that long because several ants were delayed. Those that pursued a steady pace traversed the meter route mostly in the 60–85 second range. The indications thus are that a speed of slightly over one minute per meter represents a rapid rate on a level course. Over the usual obstacles of grassy ground it is markedly longer.

The rate of travel of *Atta cephalotes* workers carrying cacao leaf sections, when the temperature was 27.3° C, was determined over a representative two-meter section of their trail in Trinidad. Six media workers traveled this course in the following number of seconds:

120—114—111—129—84—85

Two of the same size that were carrying cacao flowers traveled the two meters in 111 and 94 seconds, respectively. A maxima worker carry-

ing a leaf section made the course in 97 seconds.

The slowest speed therefore was a meter in one minute and the fastest was a meter in 42 seconds. This may be compared with the speed of the Buenos Aires ants at 16.0–16.7° C and reflects the somewhat frenzied activity of the latter, which were mostly smaller in size. It was a spring day for them and they were stimulated to maximum activity while the Trinidad ants were operating under fairly uniform conditions, modified only by rains.

Nocturnal speeds appear to be entirely comparable to those in daytime in the tropics, while in the temperate zones the lower temperature causes them to be more sluggish.

In the laboratory at 24° C, ants from a colony of *Atta cephalotes* traveled portions of an inclined plastic tube of one meter length at comparable speeds, whether going uphill or down hill. The media workers were fastest, traveling the meter tube in one minute on the average. The minima workers took longer (108 seconds on the average).

#### BIOMASS OF VEGETATION CUT BY ATTINES

The concept of the biomass or weight of a species population per unit area, is long standing (e.g., Pickles, 1937; Allee, Emerson, Park, Park and Schmidt, 1949). The extension of the concept to the total community weight per unit area (Hutchinson, 1943) was applied to the gardening ants together with their gardens and refuse collections (Weber, 1966a, b; 1969).

The biomass created by an *Atta* colony in this broad sense seems by far the greatest concentration for which any New World insect is responsible and should be compared with the large termite mounds of Africa.

A colony of *Atta sexdens rubropilosa* 77 months old was calculated to have used 5,892 kilograms of vegetation (Autuori, 1947). The refuse in the chambers weighed 475 kilograms and Autuori calculated that for every 12.4 parts of active gardens there was one part of refuse (exhausted substrate, dead ants, and associated guests).

The Trinidad study area described in chapter 6 was 18×77 m. in area or 1.386 m.<sup>2</sup> (Weber 1966b; 1969). The number of colonies of all attine ants and the population of representative mature colonies of the most abundant species were determined (chapter 6). An attine population of 170,000 adult workers was estimated conservatively to be present here one year. The living weights of the common species are given

in chapter 2. The biomass of the ants themselves can then be estimated from these data. A hectare of this type of land would contain at least 1.23 million ants of the smaller species, weighing on the average 1 mg., or a total ant weight of 1.23 kg. At least 1.77 million larger ants (*Acromyrmex* and *Atta*) present here would each weigh fully 2 mg. on the average. These larger ants would then add fully 3.54 kg. to the 1.23 kg. of smaller ants, making 4.77 kg. total biomass. However, the *Atta* colony in Panama that was fully collected (chapter 6) had 2.5 to 5 million ants weighing 6.35 kg., so that only one mature *Atta* nest in a hectare could make the approximate biomass for attines in a hectare 8–10 kg. A survey of the two same large leaf-cutters in one area of Trinidad (Cherrett, pers. commun.) showed there to be 0.62 nests per hectare in the forest and 3.00 nests per hectare in cultivated land. The data from south Brazil from Amante (chapter 6) show far greater *Atta* populations.

In summary, a biomass for attine ants per hectare of cultivated tropical land of 10 kg. seems easily possible.

This figure of 10 kg. per hectare, however, represents only a small fraction of the biomass for which the ants are responsible. The gardens and refuse piles or chambers are many times this. The estimate for the 18×77 m. study area for the *Sericomyrmex* garden biomass was 9–18 kg. and that of one *Atta* nest two years of age was 6–10 kg. (Weber, 1969). The biomass of the other attine gardens when added to the above two species would bring the total garden biomass to 25–30 kg. for this 18×77 m. area. The weights and dimensions of gardens of three *Atta* species, *Acromyrmex*, and *Sericomyrmex* are known. An average *Atta cephalotes* garden of 2,000 ml. weighs  $\frac{1}{4}$  kg. as does one of similar size in *Acromyrmex octospinosus*.

The attine garden biomass per hectare of tropical cultivated land based on the above sample figures, would become some 180 kg., but it is probable that the *Atta* contribution is underestimated and the *Sericomyrmex* contribution overestimated. South Brazil data for *Atta sexdens* and *capiguara* (e.g., Autuori, 1956a) and Amante (e.g., 1967b), respectively, indicate still greater total biomass when the gardens and waste material are considered. Autuori had one study area of 944 *Atta* colonies in a 1,123.67 hectare area and Amante found averages of 10–18 colonies per hectare. The latter estimated the



quantity of grass cut per hectare to be 52.5 kg. daily, the normal food of three cattle. He noted (1966) the possibility of 300 million nests of *Atta* in Brazil taking 745 million tons of vegetal substrate annually.

#### *Drinking by the Ants*

The production of relatively large quantities of saliva and fecal droplets by these ants, requires a supplementary ingestion of water when the protoplasm of the fungus is insufficient to meet their needs. In nature they may meet this need by cutting green leaves and biting the edges of the particles. In those species, however, that use dryish substrate, such as dead leaves or dried feces, an external source of water may be essential. When observation nests are allowed to become somewhat dry, the addition of water will cause numbers of ants to go in unison and imbibe the water. This may be viewed under the microscope under favorable circumstances. Ants have been watched through the glass ceiling as they were imbibing water condensed on the underside. The entire set of mouthparts was motionless and extended into the water. Pulsing was clearly apparent as the pharyngeal muscles acted as a suction pump. The pulsing or pumping proceeded at a steady rate with several pulses to the second. This colony at this time was using somewhat withered rose petals and stems.

The ants may also regurgitate clear droplets, holding a droplet between widespread mandibles for a few moments while another ant will imbibe it. This may be an example of trophallaxis or mutual feeding although this type of behavior seems not to be as common as in some other ants (fig. 129). Trophallaxis between the queen and the worker and between the worker and the larva seems to be much more important.

#### AGGRESSIVE AND DEFENSIVE BEHAVIOR TOWARDS OTHER ANTS

The tolerance of one species of gardening ant in nesting close to other attines is notable. The material for their gardens is generally sufficient for all and they forage by one another without hostility. This tolerance also is extended to individual ants of two species meeting each other but not to the extent that they always completely ignore one another. Ants of different species that meet in the course of their foraging may stand still momentarily, with mandibles



FIG. 129. Trophallaxis or mutual feeding between two pairs of *Atta cephalotes* workers. From the author's laboratory. (Phot. C. W. Rettenmeyer.)

slightly opened and antennae widespread; then one may give way and move off before the other. Two species of *Atta* that were nesting near each other in Panama had trails that came close to one another (Weber, 1969b). When a leaf section with ant attached was picked up by forceps from one trail, with care not to excite the ant, and placed in the trail of the other species, it fled rapidly away. Clearly it recognized the alien trail, whether on concrete pavement or on the earth surface. A large colony of *Acromyrmex lundii* foraged regularly over an area inhabited by a small and inconspicuous colony of *Apterostigma steigeri*. A media worker *Acromyrmex*, much larger than the *Apterostigma*, met one of the latter, coming up to the smaller ant with antennae widespread and mandibles slightly opened. The smaller ant stood still with antennae close to the head instead of outspread as usual. The larger ant finally moved off while the *Apterostigma* stood its ground.

There may be a moment of uncertainty in determining friend or foe when two workers of a colony of *Atta* approach one another (figs. 130, 131). The mandibles are closed as they approach and the antennae wave in the direction of each other. The apices play over each other's heads when close enough and then each may touch the antennae of the other.

The physiological state of the partners in such a meeting may be indicated by the stance of the body or by odors given off. The moist mouthparts and secretions of anal and other glands must continuously give off the odor (pheromones) characteristic of the species.



FIG. 130. Alarmed soldier of *Atta cephalotes* with numerous workers responding to her. The excretion of a mandibular gland pheromone is believed to elicit this response. From the author's laboratory. (Phot. C. W. Rettenmeyer.)

An ant that is receptive to being groomed by another will stand quietly as earlier noted. The two will touch antennae, then the groomer will go to work, starting with any part of the body. Two ants may stand head to head for several seconds, their antennae playing over the other and vibrating slightly at the apices. The mouthparts may be extended with mandibles mostly shut but the heads are usually motionless, only the antennae moving. One ant may then lightly lick a part of the head of the other.

The movements of the antennae may signify more than entomologists have determined and might repay careful study. One ant may stand between two others, the outer ants directing their antennae to it. The one in the middle is evidently able to convey its state to both simultaneously, waving one antenna briefly to each.

The chief receptors appear to be the apices of the antennae and it is always these and these only that touch whatever is being explored (fig. 184).

When, for example, an alien *Atta cephalotes* worker is introduced into an observation nest of *texana* or some other species, the ants respond instantly. In part it may be that they recognize an alien odor but it may also be that they perceive unusual movements with the eyes. Attack quickly follows. The fight is short if one ant is bigger or grabs a vulnerable part first. The mandibles are the primary weapon. There may be quick darts or jumps by the attacker but usually one grabs the other. If it grabs the vulnerable petiole connection between the mesosoma (thorax) and gaster, this usually

leads to the separation of the two parts and a quick decision to the encounter.

Ants of different colonies of the same species in *Atta* are hostile to one another (e.g., Autuori, 1941), but in *Trachymyrmex septentrionalis* colonies in the laboratory they may readily be fused with one another (Weber, 1956a). This fusion also takes place between young *Atta texana* colonies in the laboratory (Echols, 1966).

I have seen a dense file of *Atta cephalotes* carrying leaf sections and passing over the forest floor, encountering an equally dense file of the predatory army ants (*Eciton burchelli*), the two files mingling without hostility, then reforming on the opposite side and continuing their respective journeys. Two more contrasting behavioral patterns in ants can hardly be found.

An army of *Eciton vagans* which was robbing the brood of smaller ants in a drainage ditch encountered a file of *Acromyrmex octospinosus* carrying leaves. The latter had to pass the *Eciton* to get to their nest and they boldly marched through the army ant file. Some of the latter threatened or attempted to attack but the gardeners kept on with a few exceptions (Weber, 1945).

Most of the attine species usually show no hostility when their nests are disturbed but immediately start recovering the brood and fragments of garden. As the ants become larger and the colony becomes more populous the ants respond to such a stimulus by more aggressive action. The ants in some *Trachymyrmex* will attempt to bite and several may attack a finger. The *Atta* ants, however,

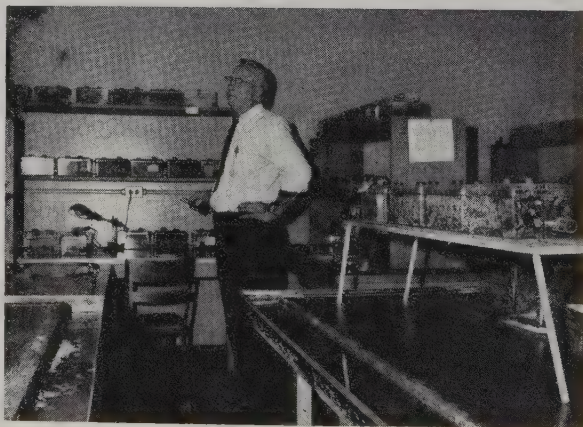


FIG. 131. The laboratory of the author showing tables in the foreground with moats (*Atta cephalotes*) and colonies of *Acromyrmex octospinosus* on the shelves at the left rear. (Phot. C. W. Rettenmeyer.)



respond dramatically when the nest is disturbed. They come "boiling" out of the large nest openings in a dense, red-brown mass and attack persistently and rapidly. One is immediately aware of their mandibles as their most effective weapon. They have a sting but it is so reduced as to be ineffective and not even easily visible (Hermann *et al.*, 1970). The mandibles, however, produce immediate results. The soldier in *Atta cephalotes* may produce freely bleeding cuts in human skin sometimes 5 mm. long (fig. 13). From both this species and *sexdens* I have commonly had my socks badly cut up, whether they were made of cotton or wool, when excavating the nests, and have had numerous thin half-moon segments cut in my leather shoes. A soldier ant has a tendency to take a firm position with its legs, then engage its mandibles in skin, cloth, or leather and hold them in position. Then by alternating pressure on each mandible in turn, a see-saw action is created which causes the mandibles to cut deeper and deeper. The largest workers do the same but to less effect.

In *Acromyrmex*, the largest workers also attack with the mandibles and bite the human skin but not to the extent of drawing blood freely (fig. 14). All large workers will grasp the skin or clothing and, while biting with one end, will discharge a brown anal deposit from the other. This is a large enough droplet to leave a distinct stain as well as odor. While I was digging up a colony of *Acromyrmex ambiguus* on the pampas of Argentina my khaki trousers became sufficiently speckled with those deposits to a point above the knees that they showed in photographs. There was in addition a musty odor characteristic of the larger attines en masse. The deposit is probably a combination of the liquid feces and the secretions of modified poison glands. Ordinarily the former would be used in manuring the fungus garden and the latter would be used in laying a scent trail.

This aggressive behavior of *Atta* and *Acromyrmex* against large animals may assist in protecting the colony against thin-scaled lizards and some mammals but not against heavily armored armadillos which tunnel into the nests in South America.

#### *Defensive Behavior of Small Species*

The species of small size do not leave the nest as aggressors and respond to possible hostile forces only by reacting at or in the nesting site.

The response of the small species to sudden stimuli may be called "jigging" (Weber, 1957a). The ants stand in one place on the garden, usually with the last four legs on it, and move up and down in a vertical plane with the rest of the body and fore legs. The response may last for a variable fraction of a minute and several ants may act at the same time while others nearby with the same exposure to the stimulus may not so react.

This jigging reaction may be interpreted as defensive behavior which may drive off small intruders from the fungus garden, such as *Collembola* and mites. Workers of *Cyphomyrmex rimosus* may respond to the stimulus of sudden light on the nest by reacting with mandibles and antennae widespread. The fore legs also may be held up and apart so that they, too, could grasp or fend off the intruder. A different reaction is for a worker to push its large head against a small, predatory ant (*Wasmannia auropunctata*) which thereupon turns about and stings the attine in the mouth (Weber, 1955). The ant is momentarily paralyzed.

A modification of the jigging behavior regularly occurred in observation colonies of *Myrmicocrypta buenzlii*. These ants responded to stimuli like sudden light, jarring of the nest, or moving one's finger over the glass cover above their garden. They would jig vertically in the same place. Jigging was not necessarily synchronized among them. Movements were so quick as to be difficult to analyze. The smallest workers of *Atta* may jig while the large ones do not.

Small species will react to small intruders by darting directly at them. In one case, a small *Collembola* lived in the nest. It would skirt the periphery of the fungus garden, then dart in and seize a bit of the substrate with fungus coating. It crawled down from the garden once and encountered an ant which immediately jumped at it with mandibles outspread. Similar behavior was noted repeatedly under the microscope in other small species and this type of behavior is also shown by the smallest individuals of the larger species.

As noted above, attines of several genera commonly nest close together in the tropics and it is usual for the mounds of the large *Atta* nests to have species of smaller genera nesting more shallowly in them. A concentration of nests of three species, a *Trachymyrmex*, a *Sericomyrmex*, and a *Myrmicocrypta* on the grounds of the

University of the West Indies in Trinidad is described in chapter 6. The workers foraged over the same ground and commonly walked near one another. One species may nest on the craters of another.

Colonies of these three species in their individual small plastic boxes were confined together in a larger box in the laboratory. Two used the same rose flowers for substrate but usually cut parts separately. Ordinarily no hostility was shown among the three.

A rarely seen incident disclosed that hostility might well be latent but ready to be shown in defense of nest or substrate being gathered. In this case a worker of *Trachymyrmex* and one of *Sericomyrmex* were walking in the general area

outside the individual nests. When they encountered one another, one suddenly jumped or darted at the head of the other with gaster curved, and the other ant momentarily fell on its side. It then ran off with movements of the head, mouthparts, and antennae indicating that it had been sprayed with an anal deposit (from Dufour's gland?). Whether glandular or fecal, the substance was obviously repellent. The ant recovered and returned to its nest area. In this situation, the mandibles of neither were involved. No use of the minute sting could be ascertained. The aggressor was the one (*Trachymyrmex*) which clearly dominated the cutting of substrate in the laboratory as well as in the field.



## 8. THE FUNGUS GARDEN AND ANT FUNGI

The fungus garden is the most distinctive feature of attine life. There are several types of gardens, and various terms have been used by entomologists and mycologists to describe the forms of the fungi. The most common terms and the six used in this book are:

*Hypha*, -ae.—any strand or filament of fungus.

*Mycelium*, -a.—a mass of interconnected hyphae.

*Gongylidium*, a.—a swelling in the middle or at the end of a hypha; derived from the Greek, gongylis, turnip (Wheeler, 1907); also called a kohlrabi head (kohlrabiknops) (Moeller, 1893) because of its similarity to the shape of that vegetable.

*Staphyla*, -ae.—a cluster of gongylidia from the Greek for a cluster of grapes (Weber, 1957). Equivalent to ambrosia bodies (Wheeler, 1907; Neger, 1908; and others) and kohlrabi bodies (Moeller, 1893, and subsequent writers).

*Bromatium*, -a.—cheese-like mass of yeast cells cultured by *Cyphomyrmex rimosus*. Wheeler (1907) used this term also for staphylae of other ants.

*Cells of fungus garden*.—Air spaces between septa or partitions of fungus gardens.

There is nothing else quite like the ant fungus garden although the termite mushroom growths are somewhat similar, as described earlier. Even the compost beds created by human mushroom growers are simple by comparison. It is strictly the creation of the ants and does not grow by itself.

Whatever the fungus will grow on is called substrate. This, however, is not a simple matter of the ants bringing in just anything to the garden. Whatever is brought in has to be rigorously treated.

The various types of gardens are described here, together with substrate used in each particular case.

### THE GARDENS

The garden of *Cyphomyrmex rimosus minutus* and its close allies consists of cheeselike masses about  $\frac{1}{4}$  to  $\frac{1}{2}$  mm. in diameter that are placed on pellets of insect excrement brought into the cavity in the soil or in rotted wood by the ants (fig. 132). The fungal masses consist of tightly packed cells that look like ordinary yeast (Wheeler, 1907) (figs. 156–161). They absorb nutriment from the moist pellets and grow by cell division to form larger and similar masses. Such a mass is picked up by the ants from time

to time and is partially eaten. The remainder is placed by them on the pellets and grows some more. If the fungus is neglected long, it starts to send out short filaments or hyphae from the exposed surfaces. These tiny masses never grow large. Wheeler called them "bromatia" and the term has been widely applied to other ant fungi of very different form. At least it is a better term than "kohlrabi bodies" that Moeller used for the form in *Acromyrmex* nests. That term means more to Europeans habitually eating this vegetable.

### THE GARDEN OF OTHER SMALL SPECIES

The gardens of other species of *Cyphomyrmex* and that of other genera of ants of small to medium size are very different. Instead of bromatia dotting insect excrement, the fungus consists of small filaments or hyphae growing from small pieces of substrate. This is insect excrement, small fragments of rotted wood, insect carcasses or pieces of leaves and flowers. The nest and garden of *Cyphomyrmex longiscapus*, known only from a single collection in the Cordillera Central of Colombia, showed an unusual form (fig. 87). The ants were nesting in a densely wooded ravine where no sun would



FIG. 132. Fungus garden of *Cyphomyrmex rimosus* consisting of small fungus masses of yeastlike cells (bromatia) speckling grasshopper (locust) feces (after Bruch).

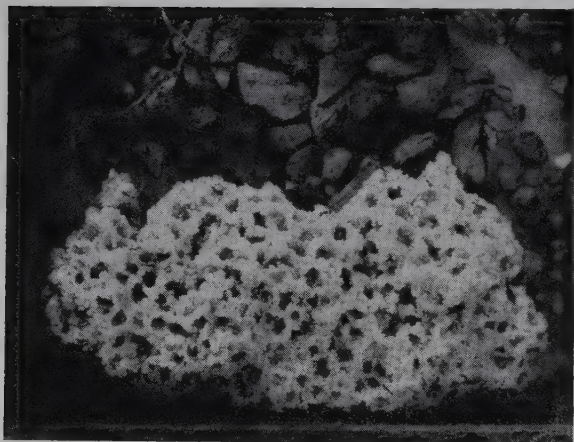


FIG. 133. Observation nest with a garden of the Trinidad *Myrmicocrypta buenzlii*.

fall on them. They had started their garden above the soil level on exposed rootlets. As the garden grew they covered it with pellets of muddy humus from 2–7 mm. thick. It speaks well for the constancy of the humidity and lack of air currents in this tropical ravine that they could develop a thriving colony in a sack of wet mud. The garden consisted of a dense white mycelial growth on a garden 40 mm. high and 30 mm. wide. The cells were 3–8 mm. in diameter and the substrate consisted of vegetal matter.

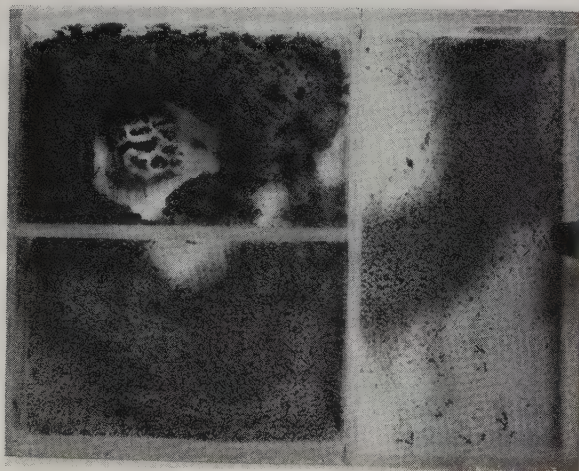


FIG. 134. Observation nest of clear plastic of three chambers connected to each other by holes. Substrate is added through the larger hole with the rubber stopper. The ants are *Trachymyrmex septentrionalis* and show the species pattern of casting out sand in the form of a semi-circular crater (see fig. 79). New Jersey.

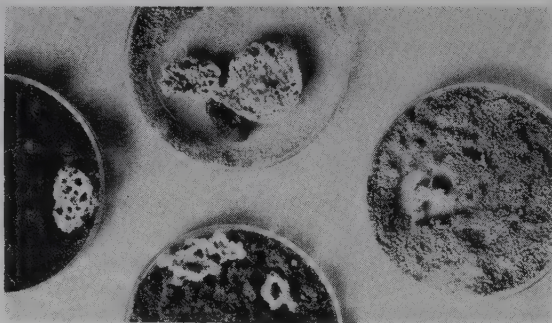


FIG. 135. Colonies of four young Guyana attine colonies in standard Petri dishes. The top center has the large queen and her young (about two months) colony and garden of *Atta cephalotes*. Below her is a colony of *Apterostigma auriculatum*. At the left is *Cyphomyrmex bigibbosus faunulus* and at the right an incipient garden of *Trachymyrmex cornetzi*.

Such a garden is usually formed in a small cavity in damp earth in the species of this and other small genera. It may be the size of a walnut (3–4 cm.) or an orange (7–9 cm.).

Small ants have small gardens and cells as a rule and a substrate of insect excrement has a different consistency compared with one of fresh leaf sections. The fungus filament (hypha) in all species is colorless, appearing white en masse, but if the substrate is dark the whole garden has a darkish cast and may appear brown or gray. The entire garden is enclosed in an extremely thin and fragile veil of hyphae in certain *Apterostigma* (fig. 139). Gardens generally may be suspended from the underside of buried rocks.

Despite the general similarity it is often possible to recognize structural differences characteristic of gardens of the ant genera.

The gardens of other species of *Cyphomyrmex*

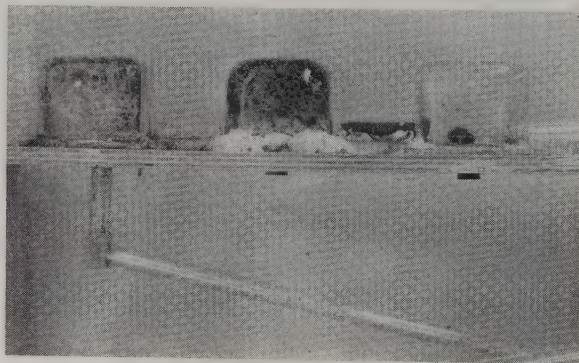


FIG. 136. Three plastic chambers of 1,600 ml. capacity set in plaster of Paris bases and connected by plastic tubes 2.5 cm. in diameter. A young *Atta cephalotes* colony from Trinidad.



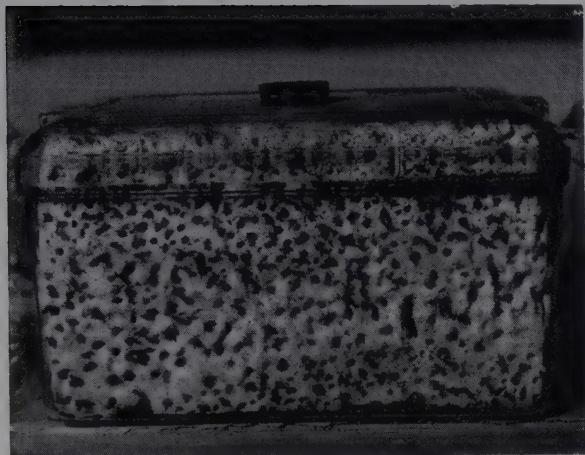


FIG. 137. Fungus garden of *Sericomyrmex urichi* filling an observation nest chamber of  $2\frac{1}{2}$ -liter capacity ( $2\frac{1}{2}$  quarts). Some ants are shown at work and are about 3 mm. long. The cover has a rubber stopper to permit adding substrate in earlier stages.

are very small (20 to 50 mm. in diameter), corresponding to the size of the ant (figs. 87, 135). Those of *Mycocepurus* are also small but looser. The gardens of the small ants of *Myrmicocrypta* are generally much larger than the size of the ants would suggest, often 50 to 80 mm. in diameter, which is the size built by ants two or three times larger (fig. 133). All three genera have gardens of fragments of vegetal matter and with cells a few millimeters in diameter. Sometimes carcasses of insects are incorporated as substrate. The garden may rest broadly on the floor of an earthen cavity, and on small stones or rootlets left in place.

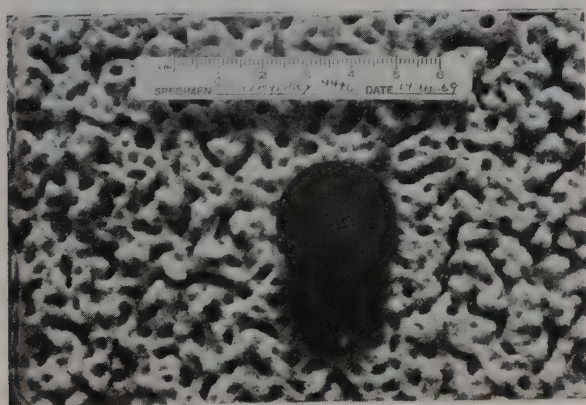


FIG. 138. Garden of the same captive colony of *Sericomyrmex urichi* from above showing the irregular cells and compact septa of the mature phase; centimeter scale.

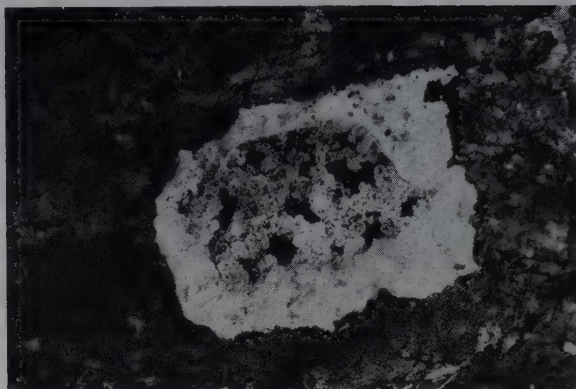


FIG. 139. Garden of *Apterostigma dentigerum* Wheeler on the underside of a log as it appeared when part of the complete mycelial veil was torn aside. Coarse pellets of insect feces or wood particles make up the loosely cellular garden. Panama.

The ants of *Apterostigma* use insect excrement; the particles of substrate are correspondingly often rounded (figs. 139, 140). Such gardens are frequently suspended in irregular spaces in rotted wood and are difficult to dissect.

The gardens of *Trachymyrmex* tend to have a laminated structure, septa being hung from rootlets entering the ceiling of the chamber (fig. 90). In other cases the fragile garden may consist of masses suspended independently from rootlets and loosely held together by mycelial threads. Some gardens rest completely on stones on the floor of the excavation.

The gardens of *Sericomyrmex* tend to be disproportionately large, like those of *Myrmicocrypta*, and the substrate is often pale golden brown, fruity, and succulent (figs. 137, 138).



FIG. 140. Garden of *Apterostigma auriculatum* grown on coarse pellets of insect droppings or wood particles. Trinidad.



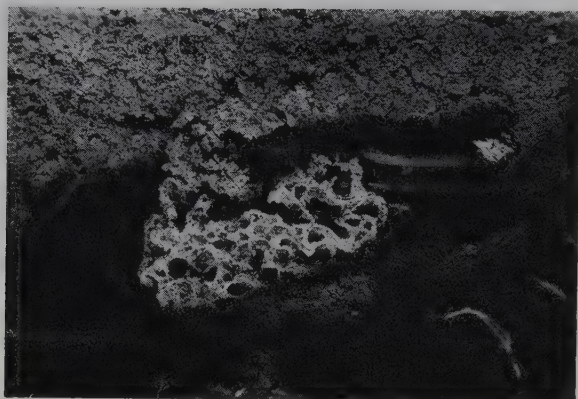


FIG. 141. Small garden of *Acromyrmex octospinosus* in a chamber in the soil. The garden is built on horizontal roots. Trinidad.

The most fragile gardens are those of species like *Mycetophylax conformis* and *Acromyrmex* (*Moellerius*) *landolti* when the ants use grass for substrate (fig. 91). The pieces are relatively long and narrow, creating an irregular mesh of cells, and the mycelium is scanty.

#### GARDENS OF ACROMYRMEX AND ATTA

The largest gardens are those of the largest ants, *Acromyrmex* and *Atta*. The former may have a single very large garden or may have a number, each of grapefruit size (fig. 141). Those of *Atta* appear to be more consistently globular and frequently of grapefruit size (10–12 cm.) but much larger in several species (figs. 106, 107).

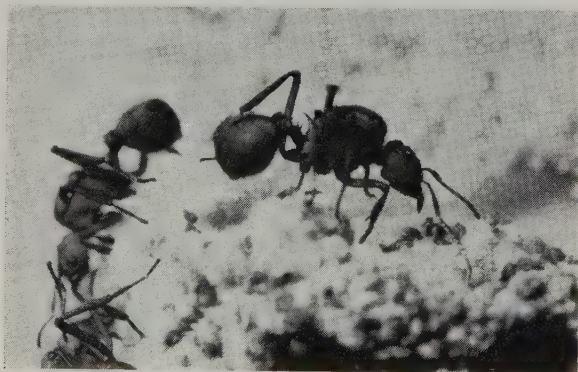


FIG. 142. Laboratory garden of *Acromyrmex octospinosus* showing two virgin females who have dropped their wings and are tending the garden. The females may behave like workers in cutting leaves and tending the garden.

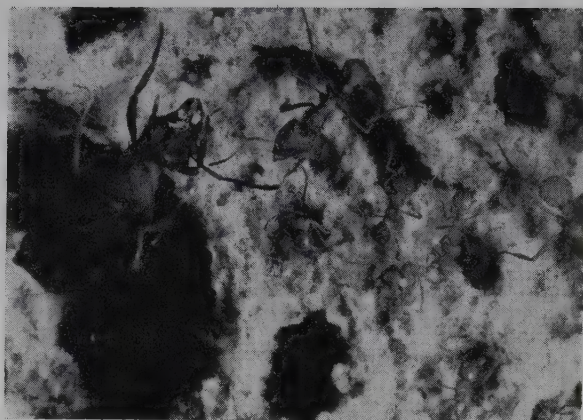


FIG. 143. Scattered white aggregates of hyphae (staphylae) on the author's laboratory garden of *Acromyrmex octospinosus*. A winged female and workers are present. (Phot. C. W. Rettenmeyer.)

#### *The Preparation by the Ants for Support for the Garden*

The preparation by the ants for support for the fungus garden can best be studied in the laboratory. Autuori (1941) described how the minima *Atta sexdens* workers go over every bit of the plaster of Paris floor of a new chamber before starting to build a new garden on it. They systematically lick the surface minutely, standing in one spot for minutes at a time. This licking must not only cleanse the surface of dirt but add saliva which at least would be favorable

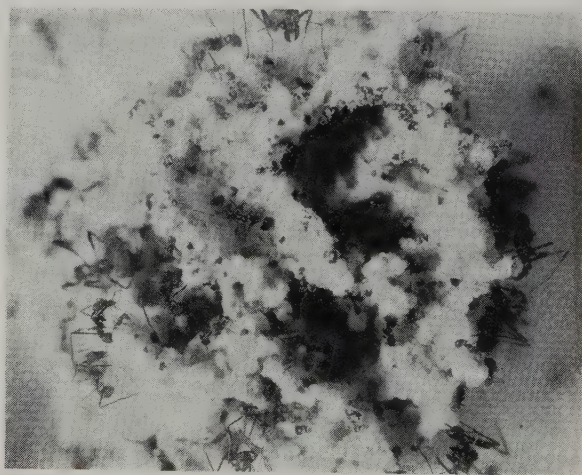


FIG. 144. Fungus garden of *Atta cephalotes isthmicola* showing ants at work, some manipulating sections of fresh green leaves, some cutting smaller sections and others tending the fungus. Newest substrate particles are dark and show recently planted islands of mycelium.



for the ant fungus. I have since verified this treatment many times in *Atta cephalotes*, also for a plaster of Paris base. The ants give the same treatment to clear plastic floors of the chamber, removing any loose material first.

Presumably the same treatment must be given in nature by all other attines to rootlets that extend through the chambers of the soil, and to stones that often are left at the base of the chamber. At any rate, roots and stones are always completely free of foreign matter when fungus gardens are attached to them. The workers commonly create a chamber in the soil that is large enough for a garden of common size (fig. 106). Later the chamber may be enlarged as the garden grows.

#### LIFE HISTORY OF A FUNGUS GARDEN

The life history of a fungus garden of *Acromyrmex* or *Atta* can best be studied in the laboratory (fig. 136). Since the temperature, humidity, and substrate in nature can be duplicated here, the history should be comparable. The laboratory results can be checked with those in nature by excavating several of the latter over a period of time but this destroys the gardens.

A mature garden of *Atta cephalotes* in nature is a honeycombed structure which is far from being homogeneous (fig. 107). Its sides and upper surface are in the form of coarse cells with thin walls. These are dark in color, appearing superficially grayish brown because of the



FIG. 145. Worker of *Trachymyrmex zeteki* placing a piece of substrate in the garden. The mouthparts below the mandibles are kept retracted.



FIG. 146. Small garden of *Trachymyrmex septentrionalis* maintained on cassava granules in a Petri dish of nutrient potato dextrose agar despite the numerous colonies of alien fungi and bacteria. The ants were able to maintain the garden of their own fungus by manuring and licking it and by removing all agar from the vicinity; yet the ants had to walk over the contaminated agar to retrieve cassava granules placed here for substrate (after Weber, 1956a, Ecology).

mycelium. The underside is contrasting in color and size of cells. It is yellow to pale brown and the cells average only a fraction of the outer cells in diameters. This part of the garden, roughly the lower half or third, is much more solid than the outer part. The compactness is due to the gradual packing in of the substrate and replacement of the loose mycelial mesh by compact fungal masses or staphylae. The septa, therefore, are thicker compared with their breadth and height.

New substrate is added only to the upper and outer parts of the garden. Whether this is of particles of originally bright green leaves or of colorful flowers, they all become dark brown in the process of handling. These particles are added to the coarse outer cells on their very rims, creating comparatively knifelike ridges.

A young, active *Atta cephalotes* colony that was afforded an abundance of rose flowers for substrate developed a new garden in a clear plastic tube, 22 mm. in internal diameter. The new garden was built up in three weeks to fill 21 cm. length of the tube. During this period it was the characteristic dark brown and loosely cellular

type. The ants placed many small larvae here in the latter part of the three weeks. The garden turned pale brown in the fourth week and the larvae were moved out to another and younger nest. Staphylae became numerous during the next week or two and the garden became irregularly reduced in its seventh week of existence. Most of the staphylae were moved to the new site with the larvae and were used in feeding them. This garden therefore had a life cycle of about seven weeks in this confined space (at 25–27° C).

The same young colony built a fungus garden in this period in a plastic container of 2½ liter capacity which duplicated the size and form of a large earth cell in nature. This became 70 mm. in diameter in two weeks and by the end of its first month it was approximately 90 mm. in its three dimensions. The lower part had then become pale brown and with small cells, many of 3–6 mm. diameter. The upper part had large and irregular cells as in nature, one being 30 × 16 mm. in lateral diameters, and others 10–15 mm. Staphylae grew in large numbers, were moved into the lower half of the garden and were fed to the larvae. The garden became approximately 110 × 117 mm. in maximum lateral dimensions and 97 mm. high by the end of its third month. It reached the plastic ceiling and was clearly a mature garden. The basal part was being removed in the first week of the fourth month, signifying the post-maturity phase. The entire yellowish base was removed during this fourth month. This garden therefore had a life of 4 months.

In the meanwhile a second *cephalotes* colony started a new garden on the plastic floor of a new container in front of a pile of sand. The ants had first given the area a thorough examination, licking it minutely as Autuori has described. After 11 days the garden was only a fraction of a milliliter in bulk but in the next 24 hours it grew to an estimated 10 ml. due to the abundant fresh rose flower substrate the ants used. The garden became 68 × 42 × 40 mm. in maximum dimensions after 26 days and, when 29 days old, it showed the pale brown base with small cells and thick walls characteristic of mature gardens. The garden was 70 × 50 × 55 mm. in its maximum dimensions on its 30th day. The corresponding bulk of 192.5 ml. from these figures would be the capacity of the smallest container that would fit it. This young

garden therefore was fully developed except in size in its 4th week.

Three months after it was started the garden was approximately 110 × 110 × 100 mm. and the basal 20–40 mm. was yellow. The cells here were small, compact, and had thick walls. Brood was confined to the upper and newer dark gray-brown cells. It had all of the characteristics of a mature garden.

The life history of laboratory gardens in *cephalotes*, *sexdens*, and *colombica tonsipes* colonies has been found to be similar to these records on many occasions, young colonies developing gardens having a life span of 3–4 months at 25–27° C.

#### FUNGUS GARDENS UNDER DRY CONDITIONS

The general environment of the tropical-ant fungus is one of high humidity. Most species nest in the soil and the ant chambers maintain a high degree of humidity except in the dry season, and even then ants maintain the humidity by digging deeper into moist soil.

The three species of *Atta* of western Panama and the Panama Canal Zone showed clear-cut adaptations to an unusually severe dry season by late March, 1957 (Weber, 1957b, 1969b). Little or no rain fell in western Panama and less than normal in the Canal Zone since mid-December, 1956. The ants foraged at a reduced rate for leafy substrate, did no excavating, and abandoned the upper tier of cells that during the rest of the year would be occupied by fungus gardens. The fungus itself consisted of a sparser than usual filamentous growth and a particularly dense form of staphylae. These, like minute white golf balls, were carried about by the ants and used as food. They would be less subject to desiccation than loose filaments. Most of the activity of the colony was sub-surface and devoted to the rearing of the annual sexual brood.

Other gardening ants of smaller size here also showed little above ground activity and did no excavating.

The New Jersey *Trachymyrmex septentrionalis* may adapt to summer drought. During the unusually dry summer of 1964, the ants that ordinarily nested on a slight rise in the pine-oak barrens moved 10–30 meters away to a level not one meter lower but in the direction of a small river, still nesting in pure sand. There was clearly more soil moisture here.



Wheeler (1917) reported an extreme situation in Arizona with the larger *T. arizonensis*. It lives in arid, stony canyons in the mountains, invariably on sunny slopes or in the bottom of the creek beds. He found a normal garden in hard, dry soil in a chamber whose walls were very dry and dusty. A dusty condition would appear incompatible with this fungus. That it was not, was probably due to the still air in the chamber and residual moisture in the substrate. The fungus did not appear to have compact staphylae when I verified his findings later there. The deserticolous *T. turrifex* and *Cyphomyrmex wheeleri* of the American Southwest appear to nest more deeply in the arid soil (Wheeler, 1907).

The fungus garden thus is a dynamic structure that the ants develop and maintain under varying conditions. The behavior of the gardening ants is similar throughout the vast range from the United States through the tropical regions to the southernmost range in Argentina, and a garden of a particular genus of ants looks much the same, whatever the latitude or ant species.

#### DETERIORATION OF THE FUNGUS GARDEN

A deterioration of the garden has been described by Stahel (1943). A huge artificial garden was made by filling 9 baskets with fungus gardens collected from several nests of *Atta cephalotes*. The baskets contained a total of about 39 kilograms (100 pounds) and were placed in one large excavation in the ground. The ants were given many fresh green leaves daily, which were immediately taken and used in building up the immense garden. The ants suddenly refused to cut the leaves and left the garden after 4 weeks. The abandoned garden collapsed and formed one large, soft and rotted mass.

I have found this sudden deterioration of the garden in my laboratory with tropical species. A sure sign is the migration of the ants to a remote and upper part of the observation nest where the air is freshest. Not only may a change take place in the ant fungus, as described below, but bacteria, yeasts and other organisms, constantly present in the succulent garden, may build up rapidly to large populations. This is clearly true of Collembola, mites, and nematode worms.

The deterioration of a nest of a colony of *Acromyrmex ambiguus* in Buenos Aires Province, Argentina, took place on typical pampas occu-

pied by cattle. No insecticide, pesticide, or other chemicals had ever been known to be applied to the whole area. It was one of several nests interspersed with more numerous nests of *A. lundii* but was a mound of thatch; those of *lundii* were the common type of soil crater or bare entrance with gardens in the soil.

The mounds were noted and several excavated the first summer I visited the area (chapter 3). All were normal. The only nest that could be found here the second summer was one surrounded by about eight thistle plants. The mound had collapsed and a musty odor prevailed as the thatch of the center was removed. This was ordinarily the site of the fungus garden and the odor was undoubtedly due to spores of a fungus. Could this have been the conidial stage of the ant fungus?

#### SUBSTRATE

The most common substrate for the fungus is vegetal material. Some of the smaller ants use insect excrement, especially of caterpillars (Lepidoptera) or wood-boring beetles (Coleoptera). Smaller ants may also regularly use carcasses of insects, often of ants. These seem to be insects that have died and fallen to the forest floor, for ant carcasses may be found in terrestrial fungus gardens of species not known to climb trees. As good a growth of fungus may be found on shiny, hard pieces of insect chitin as on succulent substrate though this is perhaps a temporary condition.

The ants (except in *Atta*) treat their own brood at times like pieces of substrate, similarly embedded in the walls of the garden cells and coated with the fungus. This is particularly the case with young pupae, which need no care until ready to emerge as callows (young adults). Larvae, when embedded, have the head capsule out so that they can easily be fed.

Many plants are known to be harvested by *Atta* and *Acromyrmex*. Moeller concluded in 1893 that in south Brazil the ants would take almost any plant. Their preference for certain ones was of course well known, since this included many grown by man. A list of plants harvested by *Atta cephalotes* in Guyana (see chapter 6) represents a sampling of native vegetation (Cherrett, 1968). The plants were those in an area of 1,194 m<sup>2</sup>. around a study nest and included 72 species, of which 36 species were attacked in the 9 weeks of study. One tree was attacked on 19 consecutive nights. The ants

would not cut the nearest specimens of a tree being attacked. The introduction of agriculture disrupts this pattern and the ants cutting cultivated plants more extensively contributes to their pest status.

The use of green leaves by *Acromyrmex* and *Atta* is the outstanding feature of gardening ant life from the human economic point of view and the quantities involved are described later. Species of the much smaller *Sericomyrmex* and *Trachymyrmex* may also cut green leaves but are of little economic importance except sporadically. Defoliation of whole trees overnight by the larger ants is not unusual. An *Atta cephalotes* colony at the edge of a commercial cacao plantation in Costa Rica was invading the trees in succession and, at the time of my visit, one tree was estimated to be one-fourth defoliated. The leaves could be gone the next day at the rate the ants were working. The ants, however, were moving on to the next instead of completely defoliating the tree. Other cacao trees were being attacked by *Acromyrmex octospinosus*, that were specializing in cutting off the flowers. The flowers in this plant spring directly from the trunk and major branches and are easily accessible to the ants. Each flower that was removed represented the loss of a potential cacao pod.

The cut leaves as brought into the nest are far too large to be used directly in the garden. They are cut into small pieces by ants standing on or beside the garden.

A piece roughly one or two millimeters in diameter, is rotated between the mandibles of a worker, or several workers may operate at opposite sides of the same fragment. As it is rotated the fragment is squeezed so that the periphery is finely scored and the juices exude. After the fragment has been reduced to a juicy mass, the worker carefully places it at the tip of the gaster and defecates an amber fecal droplet on it. This treatment is given not only to all green leaf fragments but also to dried leaves and miscellaneous vegetal material and is the final stage before the ant imbeds it in the fungus garden.

#### SUBSTRATE USED IN THE LABORATORY

The natural substrates may not be available or convenient to use in the laboratory. In 1934 I started to use the dried meal of cassava (*Manihot esculenta* Crantz, formerly known as *M. utilisissima* Pohl). Cassava, known also as manioc, farinha, and by other names, is a

starchy preparation which takes the place of wheat and rice flour in wide areas of the tropical world. The living plants are strongly favored by *Atta* and *Acromyrmex*. These ants may be so persistent in defoliating such plants that the local people may abandon the plots (Weber, 1947). The ants have not been known to attack the roots, source for the starch cassava, but are notorious for cutting the sacks in which the dried meal is kept in tropical America. This substance is taken back to the nest and used for substrate for their fungus. I have used a particular sack of the cassava from South America since 1947 and given it to a considerable variety of ants. Although the laboratory has had temporary infestations of a variety of stored products insect pests, they have not attacked this sack of meal.

Caterpillar feces of *Malacosoma americana* and *Danaus plexippus*, among others, have been used with success for certain species of ants. The higher attine genera have regularly been given many plants in season.

Roses were used at first and then a variety of other plants. These included plants from other parts of the world not normally available to the ants in nature. Among these were members of the Crassulaceae, Ericaceae, and Oleaceae. Two plants, useful as source of large quantities of leaves in recent years have been *Rhododendron* in the winter and ash (*Fraxinus americanus*) in the summer.

#### Artificial Substrate Adopted by the Ants

In 1934-1935 in Trinidad I experimented with furnishing a variety of chemical substrates that would never be available to the ants in nature.

At first they were: diastase, blood fibrin, dextrin, gelatin, peptone, hemoglobin, maltose, and egg albumin. These were given to colonies of five species of three attine genera. Maltose was taken by all five species and directly ingested. Dextrin was also taken by all and the other chemicals were picked up by three or four species. Egg albumin was ignored by all.

The same eight chemicals were furnished similarly to eight species of attines in Guyana in 1935 (Weber, 1946). Again, maltose was directly eaten and egg albumin was ignored.

Blood fibrin and hemoglobin were used as substrate by *Cyphomyrmex rimosus*, the ants planting their yeast fungus on them, and *Atta cephalotes* planted their hyphae on the particles.



The *Cyphomyrmex* similarly used dextrin and it was tasted by *Atta cephalotes*.

The ants of *Sericomyrmex harekulli* planted hemoglobin particles in their gardens. The ingestion of maltose corresponds with the known fact that these ants will occasionally ingest fruit sugar, sucrose and honey. The ants may have used blood fibrin, dextrin, and hemoglobin for passive support for the fungus as they normally use pieces of insect chitin. In such cases the fungus may grow only at the expense of the added saliva and feces. These experiments now have primarily an historical interest in view of the work of Martin, *et al.* described below.

#### *Following the History of Individual Substrate Particles*

The treatment given by the ants to substrate can best be followed by observing individual particles (fig. 145). When new substrate is placed in an observation nest, and the ants are currently in need of it, they immediately start to carve it into pieces, if it is a green leaf. When it is already of suitable size, as are most of the cassava meal granules, they carry the material at once to the vicinity of the garden. The treatment may be watched under the binocular stereoscopic microscope. An individual particle, newly placed in the garden, can always be followed for at least one day since it is glistening wet, whatever the material, and newly planted hyphae have not had time to grow into characteristic positions or lengths.

Better yet is to dye the cassava with a neutral, aqueous dye such as Neutral Red or Nigrosin (Weber, 1957a). In such cases there can then be no mistaking when a newly planted particle has acquired its islands of hyphae. Two hours after an ant had removed one black granule it had been planted with 22 discrete tufts of hyphae. The temperature was 24.5° C and the tufts remained independent of one another and with hyphae still collapsed. After a few hours these islands grew together and some hyphae were growing upright. Another dyed particle had eight tufts planted on a surface less than 2 mm. long and a third received 11 islands of the fungus on a surface less than 1½ mm. in diameter.

#### THE AMOUNT OF SUBSTRATE NEEDED FOR GARDENS

Data on the amount of fresh substrate needed for the ant gardens have been correlated with the

increase in volume of the gardens, especially in *Sericomyrmex*, *Acromyrmex* and *Atta* (Weber 1966a, b; 1969 a, b). The results indicate the considerable amount of vegetation cut by the ants and this can now be expressed in kilograms or pounds of green leaves and fresh flowers per fungus garden. It is difficult to translate the grams of fresh leaves cut to the amount of damage being done in nature. One way is for the person residing here to pick up a mass of the leaves being cut, and weigh them, allowing for the stems and leaf petioles not always being used by ants at that particular time. To such amounts must be added that wasted by the ants when they are caught in a shower and drop the sections along the trail.

A colony of *Sericomyrmex urichi* (described in chapter 6) was taken July 15, 1965, within a few weeks of beginning (figs. 137, 138). The garden was only 15 ml. on the following May, then spurted to 100 ml. by July, when it was about 14 months old. The colony used only a few grams of flowers on an occasional day until July, 1966. The ants took 10 grams of substrate in July and 15 grams in August. By the end of 1966 the ants could take 40 to 73 grams monthly in building a garden of 1,100 ml. (well over a quart). The population of ants was estimated to be 500–1,000 then and later study showed that there were indeed more than one thousand. This was a normal full-sized colony and garden except that in nature the garden would have been divided into several separate chambers (fig. 89). By the end of the third year of colony life a garden of 2,330 ml. had been produced and the 2,500 to 3,000 ants would take 89 to 152 grams of substrate monthly. This *Sericomyrmex* may well be representative of other species in the genus and perhaps in *Trachymyrmex* species. Their nests may be locally abundant and in the aggregate they would have an obvious effect on human gardens. Their activities would often go unnoticed for a time since the ants work mostly at night.

Quite different in order of magnitude is the genus *Acromyrmex*, which may rival *Atta* in over-all impact on vegetation in vast areas.

The most complete data are on colonies of *Acromyrmex octospinosus* (described in chapter 6) that were followed from the day that the queens were fertilized (figs. 51, 141, 142). Three such colonies originated from nuptial flights of July 1, 1965. The gardens grew slowly in the first months and by the following March were

only 12 to 50 ml. in volume, the ants taking one or two grams of substrate daily. During March, they could use as much as five grams on an occasional day and by July, 1966, the ants had gardens of 80, 300 and 500 ml., showing a wide variation in success. Five grams of fresh substrate could be used daily in the largest colony. The colonies used a total of 500 to 1,482 grams of substrate in the next six months in building gardens of 300 to 2,580 ml. The colonies used as much as 660 grams of substrate monthly, when they were two years old, and created fungus gardens as large as 3,600 ml. The quantity of leaves removed by such colonies in a person's garden would clearly be noticed. During three years the gardens in one colony totaled as high as 6,300 ml. and the ants used as much as 500 grams monthly. The maximum in any colony was 660 grams.

A fourth colony attained a garden of 1,300 ml. in its first year and used as much as 280 grams of substrate in a month. This rate probably comes closer to that of a successful colony in nature, than the rate of the three preceding colonies, but these examples indicate that there is much individual colony variation.

Their treatment of large rose flowers makes a spectacular demonstration. For example, two fresh roses weighing 12.3 grams were quickly cut into small pieces and 24 hours later every part, including the base of the flower and stem, was incorporated into the garden. I estimated that the ants made 125 to 150 ml. of garden per gram of rose flowers in a part of a colony kept separate from those described above. Two grams per hour from cutting to incorporation into the garden seemed to be an average in this example. A large colony in nature may take 400 grams per hour.

#### GROWTH OF GARDENS IN YOUNG ATTA COLONIES

Growth of the *Atta* gardens may be measured by increase in bulk or in weight. The single record of the amount of substrate needed for a garden showed that one kilogram of fresh leaves was used in developing one average garden of 1,200 ml., weighing 130 grams (Weber, 1966a). The fungus gardens of a few *Atta* nests have been counted, measured and weighed by Autuori (1942) and Stahel and Geijskes (1939). Of necessity, these gardens were taken from the nest, many of the ants fled and there was a variable loss of garden material.

The advantage of bringing the problem of the amount of substrate necessary to build up a fungus garden into the laboratory is that in this way variables can be eliminated. The ants in nature go out on their trails to more than one plant as a rule (Cherrett, 1968) and they may harvest at all times of the 24-hour day. One cannot be sure what the ants do with a mass of cut leaves taken underground unless he excavates, thus destroying normality. A garden as it exists in nature, with such ants and brood as it then contains, represents the biological unit of an attine nest. The actual weight of the adult ants present is a small fraction of the weight of the garden. Many of the ants weigh 0.4–3 mg. (the ones that are 2–5 mm. long) and most of the others weigh 4–7 mg. as noted in chapter 5 where the numbers in a garden are reported. The ants would weigh a total of some 10 grams in many gardens. Most of the gardens in a mature nest do not contain brood but those that do add a weight of comparatively few grams unless a sexual brood is maturing. That was not the case in any of the gardens described below.

The laboratory colonies of *Atta cephalotes* L. alluded to in chapter 6 were of known ages and brought from Trinidad. Substrate was chosen the first two years for its availability to others who might wish to duplicate these results. Fresh rose flowers were used for five or six months of the year. These each weighed up to 12 grams but were mostly 5–7 gm. Later Rhododendron and ash leaves (*Fraxinus americanus*) were used extensively. Many other plants were used for tests.

The substrate was weighed while fresh and was then immediately introduced into the nest. The ants would take 20 gm. on most days during the rose season in the first year of the colony. Rhododendron leaves were drier and took more time to cut but were used more and more as the colony grew.

Two colonies that originated in April or May, 1964, were first used. They were collected in early July, 1964. In September a total of 14 roses was given to the smaller and 20 to the larger colony, all of which were cut and incorporated into the garden as substrate. The roses weighed an estimated 85–110 and 120–160 grams, respectively. The evidence is that a small colony about five months old can harvest towards the end of this period about 100 grams of fresh leaves monthly.



The ants in both colonies cut all of the flowers, including the entire base or receptacle, stamens and pistils and incorporated all parts into the fungus garden. During the month no noticeable amount of substrate was cast out as exhausted and the gardens grew distinctly. The fungus formed large numbers of compact, white staphylae, as during dry season conditions in nature.

The colonies could take 10–15 gm. of fresh rose substrate on separate days in the first half of November. Within 20–24 hours all would be incorporated into the garden and the process of planting tufts of mycelium on the particles well underway. Ten grams of fresh substrate of other kinds could be used in December–March by each colony within less than a day. By April, 1965, outdoor substrate became available and in one month (April 17–May 17) one colony used 227 grams and the other colony 252 grams that were mostly the flowers of *Forsythia*. The

TABLE 3

	Colony A		Colony B		Colony C	
	Substrate (grams)	Garden (ml.)	Substrate (grams)	Garden (ml.)	Substrate (grams)	Garden (ml.)
1st year	3,064	4,150	2,711	1,600	3,426	2,550
2d year	6,654	6,100	5,409	5,300	6,578	4,800
3d year	5,852	7,500	4,814	5,200	6,390	7,200
4th year	7,900	12,200	4,106	6,900	6,745	11,600

ants took the pedicels, bracts, and other woody tissue associated with the flowers. They also used oriental flowering cherry flowers. The two colonies used 49 gm. and 57 gm., respectively, in a four-day period when they were then approximately one year old.

I maintained other young colonies of known ages of *Atta cephalotes*, *sexdens* and *colombica tonsipes* in the laboratory for several years each and kept monthly records of fresh leafy substrate used and total bulk of gardens attained. Laboratory conditions were identical and the temperature was kept at 25–27° C.

Three colonies of *cephalotes* in Trinidad in 1965 were noted from they day of their emergence above ground (chapter 6). They originated each from females fertilized at the beginning of May, 1965 (fig. 112). Two others from the same 18 × 77 meter area were left *in situ*. One died within the next year and the last nest of the five

TABLE 4

	Colony A		Colony B		Colony C	
	Substrate (grams)	Garden (ml.)	Substrate (grams)	Garden (ml.)	Substrate (grams)	Garden (ml.)
1st year	1,320	2,200	1,306	1,300	1,447	2,950
2d year	4,767	7,700	3,768	4,200	3,838	3,100
3d year	3,936	6,000	2,720	3,400	2,377	6,100

was partially excavated at the end of the second year. The three laboratory colonies had a record (Table 3) of substrate used and maximum garden growth.

In August, 1966, I brought similar young colonies of the Panamanian *Atta sexdens* and *Atta colombica tonsipes* to the laboratory. Three colonies of *sexdens* produced the following records (Table 4):

Two colonies of *tonsipes* produced the following records (Table 5):

The variations in substrate used and volumes of gardens among the colonies and the species are often due to circumstances such as accidental worker deaths, but also indicate a greater vigor of *cephalotes* colonies under these circumstances. A third colony of the above *tonsipes* series used 517 grams of substrate in producing a maximum garden of 800 ml., but the female died on December 29, 1966, for no apparent reason, when her garden contained 250 ml.. Her last offspring died in January, 1968. Doubtless there is much variation in the queens and their capacity to lay numbers of eggs resulting in robust workers. Variation in nature is probably much greater because of the accidents of siting of the initial chamber formed by the queen, the number of workers she first brings to maturity, their success with substrate and other factors.

Eight young colonies of *sexdens* taken in Guyana in July, 1970, varied greatly in their use of substrate and resulting garden size in their first five months. One was fused with several

TABLE 5

	Colony A		Colony B	
	Substrate (grams)	Garden (ml.)	Substrate (grams)	Garden (ml.)
1st year	980	550	1,221	2,100
2d year	1,670	3,800	3,418	3,200
3d year	2,414	3,700	2,272	3,400

hundred workers from a mature colony and far outstripped the other seven. It had a garden of 1,350 ml. when the maximum garden size in the seven was 950 ml. The smallest garden (50 ml.) was in the colony that remained for several months in a cramped container. In the first  $4\frac{1}{2}$  months they harvested from 34 to 277 grams of substrate, the latter quantity for the 1,350 ml. garden. Most colonies used 130 to 150 grams, amounts that would probably compare favorably with the situation in nature.

#### *Cycle of Substrate Removal and Addition*

The removal and addition of substrate appears to be cyclic and triggered by two factors. The primary factor is seasonal. There is often little or no gathering of substrate during the tropical dry season and the fungus grows at the expense of the vegetal matter brought in earlier. The second factor is the length of time that the substrate can be used by the fungus. As shown above, this appears to be a matter of three or four months. It will then be cast out by ants at the same time that new leaves or other material are being brought in. A Panamanian colony of *Atta colombica tonsipes* carried out several liters of exhausted substrate in June of both 1954 and 1955, discarding it on the summit of the same smooth rock (Weber, 1969b). This material was golden brown and granular. The colonies discard quantities of substrate at many other times of the year as well (fig. 111). A young colony of *Atta cephalotes* carried out exhausted substrate within a week of opening the nest to the outside.

The cycle may be considered to start with the coming of rains in the monsoon tropics, following the long, dry season. This coincides with the growth of young leaves (the "flush") of trees and this is the time of greatest damage to economic plants. After a few weeks of intensive leaf-cutting, building up new parts of old gardens and entirely new gardens, there will be a lull. After the substrate has furnished its function and is then exhausted, the next cycle begins. May and June are the times of greatest substrate gathering in the northernmost ant. The much larger *Acromyrmex lundii* of Argentina casts out considerable quantities of exhausted substrate in May and June, marking the beginning of winter in this milder climate.

Laboratory colonies also tend to be cyclic in carrying out their largest quantities of exhausted substrate and show great persistence in emptying

the material at the same site, regardless of whether it is daily removed by man or not. For example, in early October the ants of one of the above *Atta cephalotes* colonies cast out much substrate, then smaller volumes were gradually cast out in following weeks. A garden volume of an estimated 10,600 ml. was present on December 15. The ants accelerated the casting out process at the end of December for a week, reducing the total volume to 9,300 ml. The colony was then  $4\frac{1}{2}$  years old and had taken in 2,200 grams of fresh substrate in the September-December period. The sister colonies, identical in origin, had other schedules of casting out substrate.

#### *Bacteria in the Fungus Garden*

There is a bacterial flora in the fungus garden which is of course invisible under ordinary examination but which will often show up in otherwise sterile cultures on nutrient agar. Exactly what role bacteria may play in the normal garden is difficult to assess and the bacteria have not been identified. Whether the bacteria themselves could be a third partner in a symbiotic association has not been proven. Conceivably they could assist in the disintegration of some substrates. Perhaps they play a role in the digestion of cellulose.

The bacteria are regularly associated with the yeast cultures of *Cyphomyrmex rimosus*. These grow directly on moist insect excrement which contains a wide variety of organisms. The ants, as they feed, pick up these masses (bromatia) and rotate them between their mouthparts, rasping off and ingesting the yeast cells. Then they put the remainder back on the substrate or in a pile of similar masses. When these are handled with sterile needles and placed on nutrient agar the bacteria transmitted with them often overwhelm the ant fungus. Bacteria are less commonly associated with staphylae from the gardens of higher genera when they are cultured. These staphylae are treated by the ants much as are yeast masses, repeatedly handled by the ants, then placed back in the garden if they are not consumed.

There is ample opportunity for the bacteria to become attached to relatively clean ant fungal masses in both cases. The occurrence of bacteria in substrate, after incorporation in the natural garden, can also be readily demonstrated. Obviously the moist substrate in the normal humid atmosphere of an ant nest is as suitable for



bacteria as for fungi. The crucial point is that the ant fungus grows rapidly enough in the garden to tolerate a bacterial flora, if it exists.

#### *More than One Species of Fungus in the Garden?*

Superficially and under the stereoscopic binocular microscope there appears to be one type of fungus in the garden of each ant species. In artificial cultures on nutrient agar the fungus shows the same form. The cultures from *Cyphomyrmex rimosus* grow yeast cells, from *Mycetophylax conformis* grow a scanty mycelium with scattered flocculent masses and from ants of higher genera grow the staphylae of the same form as in nature.

When alien fungi appear in the cultures they grow more rapidly, form conidia, sporulate, and overwhelm the ant fungus. These are never eaten when returned to the ants.

The ant garden, then, may be said to consist of substrate with one flourishing ant fungus. If other fungi are present, they must be in the form of spores or a suppressed mycelium. The ants therefore are best said to culture selectively one fungus rather than to form "pure" cultures.

#### *Weeding as a Factor in Fungus Culture*

The cropping or removal in some manner of alien fungi has sometimes been assumed to be an important factor in the creation of the normal fungus garden. Wheeler (1937: p. 14) was only repeating the general assumption when he spoke about the media and minor workers confining themselves to the task of "weeding the fungus mycelium." This weeding would seem to be necessary in view of the constant bringing in of alien fungi and bacteria on the substrate and integument of the ants themselves. I was convinced long ago that this is not an important factor (e.g., Weber, 1947). It is instead a case of the ants creating an environment through the use of their saliva and excrement which favors the normal ant fungus (see Biochemical Aspects below).

Experimentally in the laboratory, however, the ants respond to alien fungi introduced near or on their garden by removing them quickly to their usual refuse heap. If sporulating alien fungi do develop on the garden because of too few ants to care for it, the ants may weed out the affected part. The ants retract all of their submandibular mouthparts in such a case and use their mandibles to pull out the alien hyphae.

They pause frequently to clean their fore tarsi and antennae as though conscious of a distasteful or dangerous substance.

#### EXPERIMENTS WITH ONE ANT SPECIES CULTURING THE ANT FUNGUS OF ANOTHER

I have often performed experiments in which ants of one species have been given pieces of the fungus garden of another ant genus or species (e.g., Weber 1945, 1957). The experiments generally succeed with those whose fungus in artificial culture is clearly similar, i.e. produces staphylae or other forms that are clearly alike. This is most likely to be true in interchanges between the species of *Sericomyrmex*, *Trachymyrmex*, *Acromyrmex*, and *Atta*. It is not enough that the ants eat the fungus of an alien species but they must either adopt a bit of the other's fungus garden or tend some of a culture from the other ant.

The adoption of one ant's fungus by another ant may also involve the brood. Six isolated *Trachymyrmex septentrionalis* workers and one of their pupae were added to an agar plate culture of *Atta sexdens* fungus on May 11. The pupa was a day or two old, having the integument entirely white and the eyes faint gray. There was no fungus on the pupa. Five hours later the ants had deposited 12 fecal droplets on the alien fungus and on their own pupa, the pupa now having had mycelial tufts planted on various parts of the body. The next day the pupa was surrounded by *sexdens* staphylae and hyphae and partly covered by the fungus masses that its workers had piled over it. Later in the day the pupa became clean and shiny, free of fungus, by the ants licking its integument. They had been "feeling" it all over with the apices of their antennae and standing on it from time to time. The pupa remained clean despite contamination of the nearby agar by *Pencillium* or *Aspergillus* and matured as a callow worker on May 24.

*Trachymyrmex* colonies, such as of *urichi* or *septentrionalis*, repeatedly accept a fungus garden fragment from an *Atta cephalotes* colony. The ants then proceed to care for the fragment and build up a viable garden.

Ants in early experiments ate or cultured the fungus of one another, such as *Trachymyrmex* (*septentrionalis*, *urichi*, and *cornetzi*); *Acromyrmex* (*octospinosus*); *Atta* (*sexdens*, *colombica*, *tonsipes*, and *cephalotes isthmicola*).

Some inconsistencies were later shown, such as that *Trachymyrmex zeteki* ate the fungus of

the ants in the above list but the other ants did not eat the *zeteki* fungus. Ants of *Sericomyrmex amabilis* ate the fungus of most of the above ants in the list but its fungus in turn was eaten only by two of the *Attas*. *Acromyrmex lobicornis* of Argentina adopted the garden of *Atta cephalotes* of Trinidad when it lost its own and built it up in the form of its original type. *Acromyrmex* (*Moellerius*) *landolti balzani* of Guyana adopted the garden of *A. (Acromyrmex) octospinosus* of Trinidad. It is to be expected that further study along this line will show greater flexibility among some of the ants but actual development of a viable fungus garden will usually only proceed with ants of the closely related higher genera.

I had no evidence that the ants would culture anything that was not a clear-cut ant fungus, contrary to the report of Goetsch on South American ants and gardens brought to Germany. He and Stoppel (1940) reported the consistent isolation in Germany of *Hypomyces ipomoeae* and *Fusarium* species from the fungus gardens of the Brazilian *Atta sexdens*, while those of *Acromyrmex striatus* from Patagonia yielded closely related forms. The ants utilized them repeatedly for construction of new gardens, but only when accompanied by other fungi (especially *Mucor* species). The Patagonian ants were induced to make use of *Hypomyces* species occurring on *Boletus* in Germany, again in conjunction with *Mucor*, so that the provision of specifically South American strains seemed unnecessary. This type of work needs to be repeated before it can be correlated with the natural situation. A starved ant or a starved colony will of course eat a variety of foods to keep alive and if they are kept chilled they need little food to survive. My experience has been that the ants that have a garden of their own fungus are immediately repelled by a non-ant fungus of ordinary contamination type (e.g., *Aspergillus*, *Penicillium*, *Trichoderma*, *Mucor*).

#### BIOCHEMICAL ASPECTS OF THE ANT DEPOSITS

Early in these studies I ascribed significant roles to the ant excretions (salivary and anal) because these were continually applied by the ants to the gardens in every species. In Wheeler (1937: p. 14) I referred to "nutritive fecal droplets and the mycelium which grows on them," and later (Weber, 1941: p. 98) stated that "these particles (substrate) are manured

with the ant's liquid excrement, the latter probably contributing an important part of the proteins and other foods necessary to the metabolism of the fungus. Later (1947b) I said "that the chemical environment created by the malaxated (chewed) substrate and the ant fecal droplets favors the particular fungus grown by the ants." Other aspects of the ant's behavior were considered in later studies. These concepts led Martin and his associates to undertake studies on the biochemical basis of the fungus-attine ant symbiosis (Martin and Martin, 1969a; Martin, 1969, 1970). They found that the two major nitrogenous components in the rectal fluid of *Atta colombica tonsipes* were allantoinic acid and allantoin. Significant quantities of ammonia and free amino acids were present, including all 21 of the common natural amino acids. Glutamic acid, histidine, arginine, proline, lysine, and leucine made up 82 per cent (by weight) of the total amino acids.

These substances are clearly beneficial to the growth of the ant fungus but have to be supplied repeatedly because they are nutrients that the fungus consumes. The saliva and the fecal material were also examined for proteolytic enzymes. No protease activity was detected in homogenates of the salivary glands, mandibular glands, maxillary glands or postpharyngeal glands. Significant protease activity was detected only in the contents of the midgut and rectum. Seven attine species were examined and in every case the level of protease activity in the rectal fluid was several times higher than in the contents of the midgut. No antibiotic activity was found.

The fecal material of the ants was thus shown to provide the ant fungus with both a nutrient supplement and a proteolytic enzyme supplement. My early suggestion that the ant deposits are possibly growth-promoting (Weber, 1947b, 1955c, and 1956a) remains to be proven.

Herbicidal or antibiotic activity of the metapleural glands of *Atta sexdens* and other ants was proposed (Maschwitz, *et al.* 1970, Schildknecht and Koob, 1970, 1971). They reported the secretion of phenylacetic acid, indolylacetic acid, and B-hydroxydecanoic acid from the worker ants and suggested that these secretions enabled the ant fungus to thrive rather than alien fungi in the garden.

Clearly, the maintenance of one flourishing fungus in an ant garden depends on various factors.



CHEMICAL CONTRIBUTIONS OF THE  
FUNGUS TO THE ANTS

Martin *et al.* (1969a, b) have also determined the chemical contributions of the fungi to the ants. The fungus cultured by *Atta colombica tonsipes* provides the ant with a rich and complete diet. More than 50 per cent of the dry weight of the fungus is available as soluble nutrient. Carbohydrates make up 27 per cent of the dry weight of the fungus; free amino acids 4.7 per cent; protein-bound amino acid, 13 per cent; and lipid, 0.2 per cent. The carbohydrates consist of trehalose, mannitol, arabinitol, and glucose. No polysaccharides are present. The lipid fraction contains ergosterol as the major sterol.

It is clear that the fungus could provide the ants with an excellent diet and this evidence tends to substantiate the reliance in nature of the ants on their fungus.

The fungus grown by *Atta sexdens rubropilosa* has been investigated for antibiotic activity and, in the process, crystals formed by the fungus have been described (Borzani, 1960; Borzani,

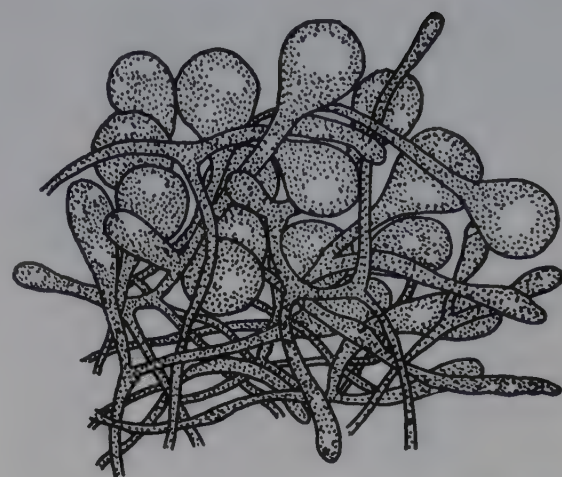


FIG. 148. A staphyla of *Acromyrmex* (*Moellerius*) *heyeri* (after Bruch).

Vairo and Pozzi, 1961). The crystals form between the hyphae in culture. They have also described a variety of culture media for the fungus of this ant, referring to the fungus as *Rozites gongylophora*. No antibiotic activity was described.

## BIOCHEMICAL ASPECTS OF THE ANT FUNGUS

The fungus of *Atta colombica tonsipes* was cultured by Martin and Martin (1969a), Martin (1970) from an inoculum that I supplied to them. This culture was also furnished to Robbins for comparison with other cultures in systematic studies (Robbins, 1969). The growth and biochemical characteristics of the fungus were investigated by the Martins. It grew poorly in the culture media on which the nitrogen was supplied as a protein (such as casein, lactalbumin, or zein) but well in media in which the nitrogen source was a hydrolyzate of the same proteins. They concluded that the ant fungus lacked the full complement of proteolytic enzymes necessary to digest the polypeptides of the normal substrate. The ant fungus, however, contributes the cellulose-degrading apparatus to this mutualistic association (Weber, 1957a; Martin and Weber, 1969). I have cultured the ant fungi on ground rose plants (flowers, buds, leaves) in 2 per cent non-nutrient agar in sterile flasks. The fungus of *Apterostigma dentigerum* grew to the top as a large, flocculent mass. Fungi from *Atta sexdens* and *Sericomyrmex amabilis* also grew well. This shows a greater independence of the fungus than indicated above.

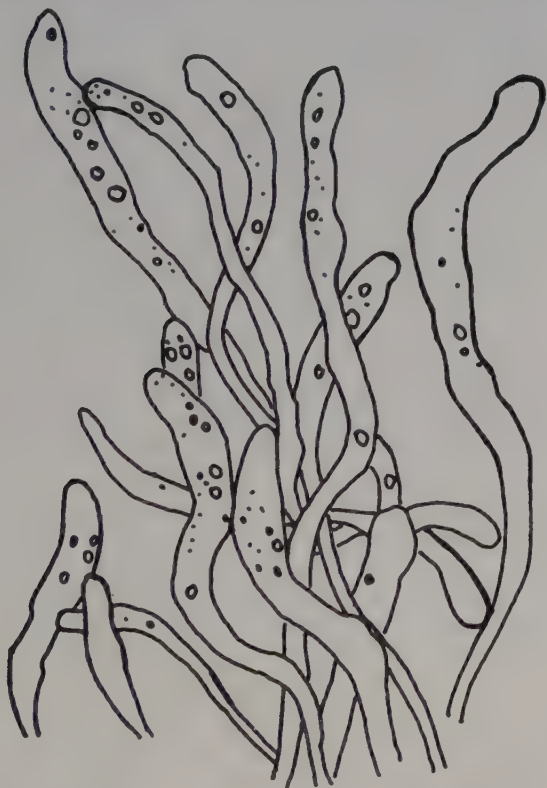


FIG. 147. A cluster of somewhat inflated hyphae of the fungus of *Apterostigma bruchi* (after Bruch).

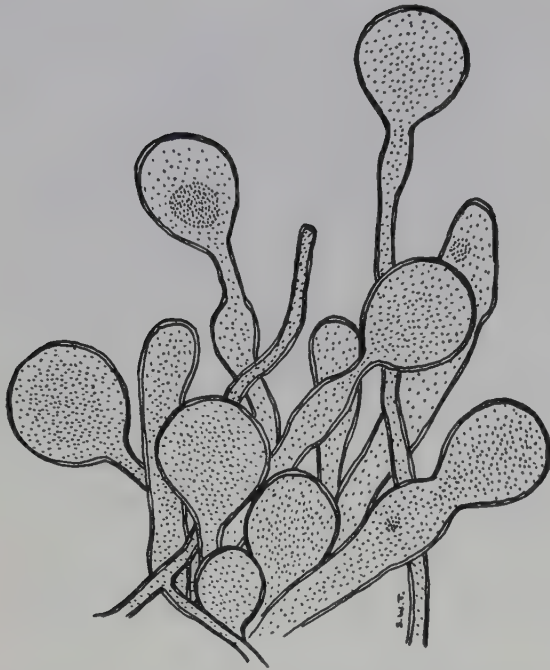


FIG. 149. A cluster of inflated hyphal ends (staphyla) freshly removed from the garden of *Trachymyrmex jamaicensis*.

Robbins (pers. commun. 1971) has had similar results.

#### YEAST CELLS OF CYPHOMYRMEX RIMOSUS

Wheeler (1907) described the fungus of the ant *Cyphomyrmex rimosus* as *Tyridiomyces formicarum* and assigned it provisionally to the order Exoascaceae (spelled Exoaceae by Wheeler), then including the yeast fungi. *Tyridiomyces* has since been assigned to the Fungi Imperfecti.

Wheeler's descriptions agree well with my fresh and cultured material except in size; it

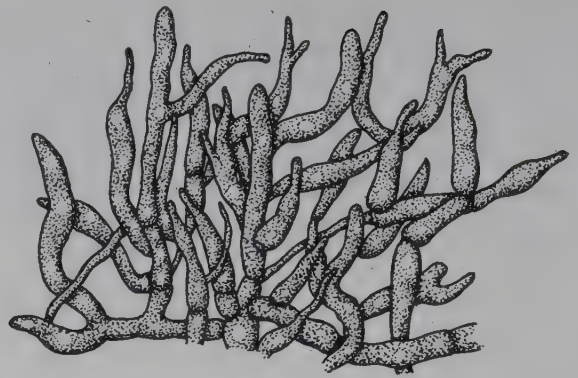


FIG. 150. A cluster of somewhat inflated hyphae, a staphyla or a "kohlrabi body," of the fungus of *Cyphomyrmex strigatus*, after Moeller.

appears that his figures must be multiplied by ten.

Representative cells were about  $12\ \mu$  in diameter (figs. 156–161). A cell of  $15\ \mu$  in diameter at the moment had a bud of  $11\ \mu$ . Wheeler did not describe hyphae growing from the cells but this was regularly the case in my cultures. A pyriform cell  $9\ \mu$  wide  $\times$   $15\ \mu$  long had a hypha  $23\ \mu$  long and  $2\text{--}3\ \mu$  thick. It had one septum near the apex. Another pyriform cell had a hypha growing from it that was slightly longer than the cell. The hyphae may rarely bud or branch.

The cells are more irregular, sometimes lunate and often smaller when a pure culture is prepared on nutrient agar. The surface of the culture bears a fine coat of upright hyphae.

#### ANT REACTIONS TO SPECIES OF LEPIOTA

The reactions of the ants were tested in 1966 against free-living species of *Lepiota* sent by W. J. Robbins. These were cultures on nutrient agar plates and were supplied to workers that

TABLE 6  
RESPONSE OF ATTINES TO FREE-LIVING SPECIES OF *Lepiota*

Fungus	<i>Myrmicocrypta</i>	<i>Sericomyrmex</i>	<i>Acro. oct.</i>	<i>Acro. lob.</i>	<i>Atta</i>
<i>amiantina</i>	neutral	accept. (2)	accept. (3)	accept. (2)	accept. (2)
<i>carcharius</i>	neutral	accept. (2)		accept. (3)	
<i>exoriata</i>	neutral			accept. (3)	
<i>lutea</i>	neutral	accept. (2)			
<i>naucina</i>	neutral		accept. (3)	accept. (2)	accept. (2)
<i>nigrocinerea</i>	neutral		neutral		
<i>procera</i>	neutral	accept. (1)?	accept. (3)	accept. (3)	
<i>rhacodes</i>			accept. (3)		



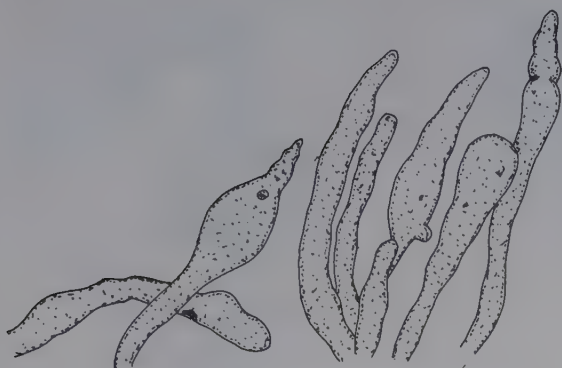


FIG. 151. Hyphae from *Atta cephalotes isthmicola*.

had been isolated the day before on damp filter paper. Several specimens of each ant species were used and the degree of acceptance noted. Three major types of responses are ordinarily recognized when attines are tested with alien fungi: (a) Positive rejection, shown by the ants moving their antennae about and avoiding the fungus. (b) Neutral reaction, the ants ignoring it. (c) Acceptance. Acceptance may be of three different degrees, (1) from a slight feeling of it with the apices of the antennae, (2) through a slight tasting to (3) a complete and rapid acceptance shown by the ants immediately eating it.

The ants were *Myrmicocrypta buenzlii*, *Sericomyrmex urichi*, *Acromyrmex octospinosus*, *Acromyrmex lobicornis* and *Atta cephalotes*. The fact that the *Acromyrmex* species accepted various *Lepiota* species indicates that their own fungus might have been taxonomically close to them.



FIG. 152. A cluster of inflated hyphae (staphyla) from *Trachymyrmex septentrionalis*.

The ants were similarly tested in 1971 with cultures of *Lepiota* and related fungi, with the assistance of Annette Hervey and Ina Wong. These were furnished by Robbins and Clark Rogerson. Two of the ants (*Acromyrmex lobicornis* and *Atta cephalotes*) came from the same colonies used earlier. Other species were similar (*Sericomyrmex urichi* and *Acromyrmex octospinosus*) and three were new (*Trachymyrmex septentrionalis* and *urichi* and *Atta sexdens*). The

TABLE 7  
RESPONSE OF ATTINES TO FREE-LIVING SPECIES OF *Lepiota* AND RELATIVES

[illegible]

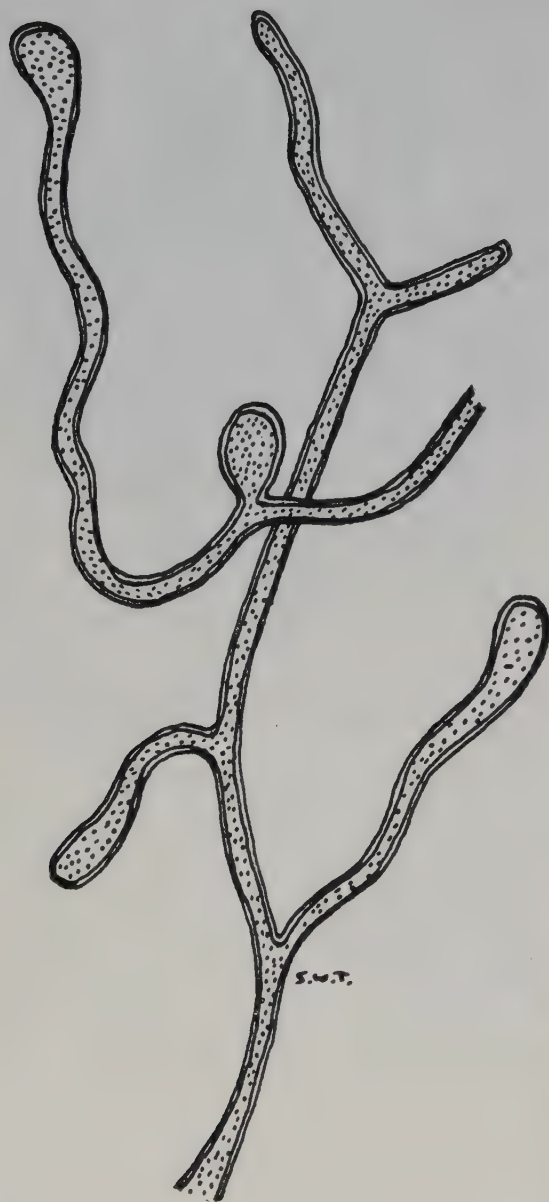


FIG. 153. Ends of two hyphae from *Trachymyrmex jamaicensis*, showing stages in the development of inflations.

added fungus genera were *Leucoagaricus naucina*, *Pluteus nanus*, and *Cystoderma* sp. The criteria were as before. Responses are shown in table 7.

The control consisted of a similar size block of potato dextrose agar of the same formula as that on which the fungi grew.

Ants that were tested to a lesser extent were *Atta laevigata*, that accepted (Grade 2) *Lepiota naucina* and later *L. lutea*, CBS 72, and accepted



FIG. 154. Conidial form of fungus found under certain conditions in the garden of *Trachymyrmex septentrionalis*. The ants immediately leave such gardens.

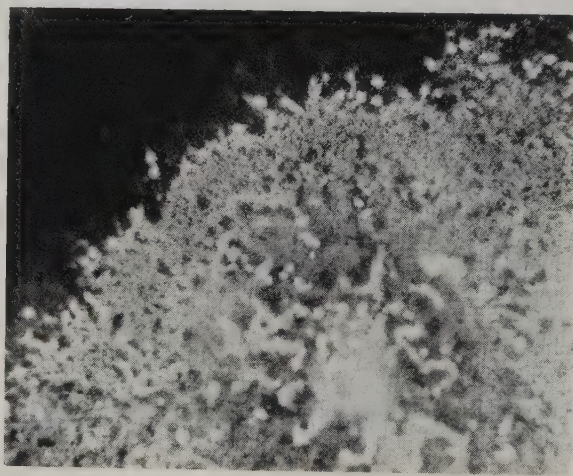


FIG. 155. A normal culture on nutrient agar of the fungus of *Trachymyrmex septentrionalis* showing the simple, threadlike hyphae and the clusters of inflated hyphae or staphylae. These clusters grow in the gardens of higher attines in nature.





156



157



158



159



160



161

FIGS. 156-161. The fungus of *Cyphomyrmex rimosus minutus* growing as a yeast in the garden and as a mycelial growth on the brood or in artificial culture. The smallest cells are 8 microns in diameter, and hyphal projections are 2 to 3 microns wide. (156) Typical yeast form in a bromatium of the ant garden. (157) Yeast cells, one extending a hypha. (158) A cluster of seven cells from the skin of an ant larva, three of them extending hyphae. (159) Hyphae growing and forking from yeast cells. (160) Compact mass of cells and hyphae growing on the skin of an ant larva. (161) Yeast cells growing on cassava granules in an active ant observation nest.

(Grade 3) *Lepiota morgani*, and *Atta colombica tonsipes* that accepted (Grade 1) *Lepiota naucina* and *morgani*.

The fact that none of the above list of fungi was rejected by any of the ants suggests that these higher genera of ants culture fungi that are at least somewhat related.

#### CULTURING THE FUNGUS

My primary objective in culturing the fungus on artificial media was to develop an identifiable

stage for the professional mycologist to examine. Little that is distinctive from his point of view is to be found in the fungus garden. My secondary objective was to keep the fungus growing in tubes or flasks that could be used to feed the ants in experiments. For purposes of verification, it is advisable to test an artificial culture from time to time by giving samples to the ant species that originally cultured it to make sure that it is the same. The ants will immediately accept it if it is the same.

I used standard mycological and bacteriological techniques in culturing. A transfer chamber where the air can be sterilized is ideal. I have been successful starting cultures in the interior of Guyana in 1936, making fungus transfers to sterile agar tubes in the early dawn, when the air would be still and saturated with moisture. Later in the New Jersey Pine Barrens I had some success by transferring pieces of garden directly to sterile nutrient agar petri dishes at the nest sites, then making later transfers from these in the laboratory (Weber, 1956a).

#### HYPHAE

The hyphae in nature form a tangle of threads covering the ant brood and the substrate. They do not grow aerielly because of the attention of the ants, but irregularly close to the surface. In artificial culture or when the ants are removed the hyphae may grow straight into the air. These threads, appearing white to the naked eye, are nearly transparent when placed in fluid on a microscope slide. They are mostly some 2-6 microns in diameter among the smaller ant genera and 6-10 or more microns in *Atta*. Usually hypha will course irregularly, branching occasionally and, when producing staphylae, will suddenly or gradually develop inflations, all usually without producing septa. Cultures from three ant genera had hyphae growing at the rate of 9 to 28  $\mu$  per hour at 23-26° C. Clamp connections (typical of basidiomycetes) were rare and appeared most common in an *Apterostigma* fungus. The individual swellings or gongylidia are easily visible to the naked eye as bright pinpoints of light (fig. 155). In *Trachymyrmex septentrionalis* these may be five times the diameter of the hypha or about 27 by 46 microns as an average.

#### STAPHYLAE

The staphylae, or aggregates of swollen hyphal tips (gongylidia) are easily seen with the naked eye as masses of compact fungus (fig. 143). The average size was 0.40 by 0.48 mm. in 10 examples of the fungus of *Atta cephalotes isthmicola*.

#### EARLY CULTURING RESULTS

I started culturing experiments in Trinidad in 1934-1935 with the collaboration of the mycologists there (Drs. C. W. Wardlaw and H. Briton-Jones). They were the first cultures to be made with these ant species and the contaminants were identified by the mycologists.

Clusters of bromatia from *Cyphomyrmex rimosus* in sterile tubes and flasks of potato dextrose and of maltose-peptone agar (the latter pH2.8) were overwhelmed by alien fungi but before they were, the bromatia had multiplied by budding. A vermiculate growth of the ant fungus grew in one (Weber, 1945). Contaminants included *Trichoderma lignorum*. Later inoculations produced pure cultures, one being sent to England by Briton-Jones.

The common bread mold, *Rhizopus nigricans* (*Mucor racemosus*) was one of the contaminants of cultures of the fungus from *Mycocepurus smithi* and *Mycetophylax conformis*. Contaminants of the latter also included *Penicillium*. Cultures of the fungus of *Myrmicocrypta buenzlii* had *Aspergillus versicolor*, *Fusarium*, and *Cladosporium* as contaminants. These were ignored by the ants when returned to them. Cultures from other Trinidad attines (Weber, 1945) developed similar contaminants. Pure cultures of fungi from these ants were turned over to D. Linder upon my return to Harvard in 1935 but were lost after his death.

#### LATER CULTURING RESULTS

I resumed culturing of ant fungi in the 1950's from many ant species from Panama and particularly at the University of Wisconsin in 1955-1956 with K. B. Raper, as summarized below.

#### Culture Media

A variety of culture media was used and a number were considered satisfactory for growing the vegetative form. Sabouraud's dextrose agar, for example, permitted a growth in which the staphylae or clusters of inflated hyphae occurred as in nature. These were as equally acceptable to the ants as those from their fungus garden in nature.

During a two-month experiment the following media were used, with the ant fungi showing the best growth in parenthesis: Sabouraud's dextrose agar (*Atta*, *Trachymyrmex*, and *Sericomyrmex*) (fig. 155); potato dextrose agar (*Apterostigma*); pine and sweet gum wood blocks as used routinely by the U. S. Forest Products Laboratory (*Cyphomyrmex rimosus* and *Apterostigma*); pine wood sticks in 2 per cent agar or in malt agar (no especial advantage); malt extract (Trommers) and 2 per cent agar (*Cyphomyrmex rimosus* and *Apterostigma*); garden humus (poor); honey peptone (*Atta*, *Mycocepurus*, and *Aptero-*



*stigma*); Rose leaf mash in 2 per cent agar (slow growth for all); oats and wheat (good for the general spectrum of ant fungi) (figs. 165-169); steep agar (corn) (generally poor); Raper's MY (peptone-malt-yeast extract-dextrose) (*Apterostigma*); Czapek's (poor for most ant fungi).

### Culture Temperatures

Duplicate cultures on Sabouraud's and potato dextrose agar were maintained during the above experimental period at three temperatures; 20° C, room temperature kept at approximately 25° C and at 30° C. The cultures came from ants of six genera (*Mycocepurus*, *Apterostigma*, *Sericomyrmex*, *Trachymyrmex*, *Acromyrmex*, and *Atta*) totaling 11 species. Both 20° and 30° C proved to be too extreme although 20° was generally better than 30° C. Only the fungus of *Apterostigma mayri* grew well at all three temperatures and the best was at room temperature.

### REFERENCE AND STUDY COLLECTION OF ANT FUNGI

W. J. Robbins set up a culture collection at the New York Botanical Garden termed the Weber Ant Fungi collection (Robbins, 1969). This consists of 25 cultures which I have sent to them in recent years from ant colonies from New Jersey, Trinidad, Tobago, Panama, and Argentina. There are 25 cultures bearing the prefix W for the culture collection and my permanent field note numbers originally attached to the ant colonies. One is from *Azteca*, a carton-building non-attine and is not further considered here. There are the fungi from two *Cyphomyrmex*, one *Mycetophylax*, two *Myrmicocrypta*, two *Apterostigma*, one *Sericomyrmex*, four *Trachymyrmex*, three *Acromyrmex*, and three *Atta* species. These have all been tested repeatedly by returning samples to the ants that originally grew them. All have been repeatedly accepted as the ant's natural fungus since the first culture was prepared in 1963. All continue to grow in culture as they do in the ant nests, with similar hyphal developments such as staphylae (fig. 170).

Two cultures added in 1970 are from *Acromyrmex* (*Moellerius*) *landolti balzani* Emery and *Atta laevigata* F. Smith from the Rupununi Savannahs, Guyana.

### REACTIONS BETWEEN ANT FUNGI IN CULTURE

Sterile Sabouraud's or potato dextrose agar flasks were inoculated with several ant fungi in experiments lasting as long as six months. The

resulting growths had no obvious reactions at their borders where they met, such as ridges that might indicate sexual strains, for example. The results were as follows:

1. Fungi from three species of *Atta* (*sexdens*, *cephalotes isthmicola*, and *colombica tonsipes*) grew together and formed one homogeneous mass. All were producing staphylae before fusion, as in nature, and these continued to grow without obvious reactions with one another.

2. Fungi from two colonies of *Atta sexdens* from the same area but taken a year apart formed discrete boundaries but without reacting.

3. Fungi of two species of *Atta* (*sexdens* and *colombica tonsipes*) with that of *Trachymyrmex septentrionalis* grew equally well, the latter two having dense growths of staphylae; the *sexdens* had a more irregular growth and tan pigment as in its other cultures at this time.

4. Fungi from four ants (*Cyphomyrmex costatus*, *Atta cephalotes isthmicola*, *Trachymyrmex septentrionalis*, and *Apterostigma dentigerum*) grew together but the *costatus* fungus overwhelmed all but that of *dentigerum*.

5. Fungi from four ants (*Apterostigma mayri*, *Mycocepurus tardus*, *Sericomyrmex amabilis*, and *Trachymyrmex septentrionalis*) produced no recognizable reactions with one another. The *Apterostigma* fungus grew earlier, then tended to grow over the edges of the *Sericomyrmex* and *Trachymyrmex* fungi. The latter had a flattened abnormal growth without distinct staphylae.

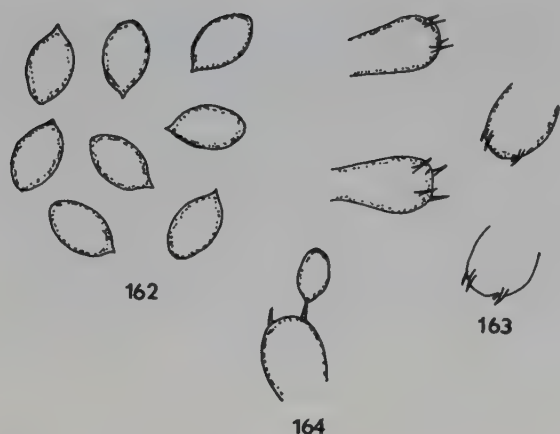
6. Fungi of three ants of closely related genera (*Trachymyrmex septentrionalis*, *Atta colombica tonsipes*, and *Acromyrmex octospinosus*) grew equally well and produced luxuriant staphylae.

### CULTURES DEVELOPING SIGNIFICANT STAGES

My cultures that produced apparently early stages in sporophores are described below, including the first to mature.

#### STROMATIC FORMS OF THE CYPHOMYRMEX RIMOSUS FUNGUS

A culture started on Sabouraud's dextrose agar, December 22, 1957 was used for transfers on the twenty-sixth. By the thirty-first they had produced crystalloid growths, like those covering the brood, and unusually long, upright hyphae. Cultures on January 10, 1958, appeared white, dense and with a low mycelial growth. Slimy areas (yeast or bacteria?) in several cultures were overgrown by the hyphae. Transfers were



FIGS. 162-164. Production in culture of the first fruiting stages of any ant fungus known. The fruiting stages are necessary for identification, and we can tell that the fungus is a species of *Lepiota* considered to be a new species by Locquin and to be the same as Moeller's *Rozites gongylophora* by Heim. From a colony of *Cyphomyrmex costatus* Mann and the fungus was grown on sterile oats (after Weber, Ecology, 1957). (162) Spores 5 by 8 microns. (163) Basidia 10 microns thick. (164) A basidium with spore attached.

made to alfalfa hay-2 per cent agar 500 cc. flasks on January 25 and the growth was fine and flocculent by February 6. Thin hyphae showed branching but with no clamp connections. Cultures of this type were ignored by the ants of the same colony from which bromatia were originally taken. A transfer was made on March 14 to a 300 cc. flask of wheat and plain agar. This developed massive black sclerotia by April 16. Samples of both types of fungus on agar were given to captive colonies of *Cyphomyrmex rimosus*. The ants licked the moist agar adjacent to the fungal growths of both types and clearly ingested fluid. When pieces of the sclerotic growth were presented to foraging ants in nature they merely and momentarily explored them with their antennae, then passed on. The white hyphal growth, however, elicited a licking response that lasted somewhat less than a half-minute. This seemed to be a significant indication that it was the true ant fungus although in an abnormal form.

Little change in the cultures was noted during the remainder of the year. On January 8, 1959, the wheat flask of March 14, 1958, had sclerotia which were later examined by mycologists and pronounced to have early resemblances to a *Daldinia* and later to *Xylaria*. Unfortunately more identifiable stages did not mature.

#### THE FUNGUS OF *CYPHOMYRMEX COSTATUS*

Early in 1956 the first successful culturing of an ant fungus to maturity was obtained from colonies of *Cyphomyrmex costatus* (Weber, 1957a). The ants culture the fungus in the form of fine hyphae that lack the enlargements (gongylidia) of higher attines. Four ant colonies were collected in Panama on June 25-27, 1955, and cultures of the fungus started from two of the ant colonies. Sporophores were reared from cultures of both of the first two colonies, reducing the chance that a sporophore could have come from some accidental fungus.

The cultures were grown on a variety of nutrient agars (potato-dextrose, Sabouraud's dextrose, Czapek's, malt, etc.) and other media (wood blocks, sterile soil, ground rose petals, oats, and wheat). It was the cultures on oats and wheat that produced the sporophores (figs. 165-166).

An Erlenmeyer 125 cc. flask of sterilized oats, inoculated November 15, 1955, and kept in a darkened cabinet, developed the first sporophores. For a month (21°-25.6° C except temporary minima of 18° on December 11 and 12) it developed the usual fluffy, gray mycelium



FIG. 165. Erlenmeyer 125 ml. flask with incipient sporophores on January 11, 1956.



characteristic of artificial cultures of this fungus but later in December the oats became coated in places with a denser white form as well, forming white nodules on the surface of the culture. There was an increasing accumulation of these nodules by January 3 (21°–25° except for a few hours of 19° in the interval) in an otherwise extensive but thin mycelium. Several nodules took an elongated, upright form on the next few days and resembled standing oat grains of flat white color, then they started darkening at the apex of each. There were four with apices constricting from the body as grayish caps by January 7.

One developed an early indication of gills in the form of short ridges on the underside of the pileus by January 13.

No further growth of the first took place after January 16 and it gradually darkened and degenerated. A new cluster of incipient sporophores started by January 18. There were about 15 nodules in a rosette, each about 2 millimeters high, elongating and attaining a reclinate to upright position.

By January 21, 11 projecting sporophores with the lead-gray pileus clearly differentiated and about 2–3 mm. high, as in the first series, developed; four others were smaller and grayish buff. One clearly outstripped the others in rate of growth the next day and on the twenty-fourth it had a total height of about 23 mm. Others developed below the first series but failed to grow further. The longest sporophore was fully 59 mm. long and 3–4 mm. in diameter and another expanded its pileus to a spread of 7 mm. on the twenty-fifth. The underside of the latter was clearly white and with radiate lamellae.

Two sporophores developing on January 26 were mature basidiocarps. Gills and the upper surface of the pileus were white except for scales which were grayish brown. These scales consisted of swollen hyphae comparable to those in natural ant gardens but with reddish brown pigment. The basidiocarps were sent at the suggestion of K. B. Raper to the mycologist, Alexander Smith. The latter made careful measurements and descriptions, then referred me to the French specialist in Paris, Marcel Locquin, who was the authority on the genus *Lepiota*, to which the fungus belonged. Dr. Locquin pronounced them to be a new species.

Heim (1957), however, concluded from a study of the Locquin specimen that the fungus



FIG. 166. Mature fruiting stages from the above flask on January 26, 1956, and showing the crowded caps or pilei.

was the same as Moeller's of 1893 and proposed the name *Leucoprinus gongylophorus* (Moeller) for them. *Leucoprinus* is a segregate of *Lepiota* (Rogerson, pers. commun.).

Sporophores of the same fungus were produced in the New York Botanical Garden from cultures of the Trinidad ant, *Myrmicocrypta buenzei* (Weber, 1966a). These matched Smith's description of the Panamanian *Cyphomyrmex costatus* in every detail (Robbins and Rogerson, pers. commun.).

If these two ant genera and Moeller's *Acromyrmex* of Brazil are indeed culturing the same fungus it suggests that the evolution of the ant genera took place after their ancestor developed the symbiotic relation with a fungus or that the fungus occurs in the wild and has been adopted independently by these different ants.



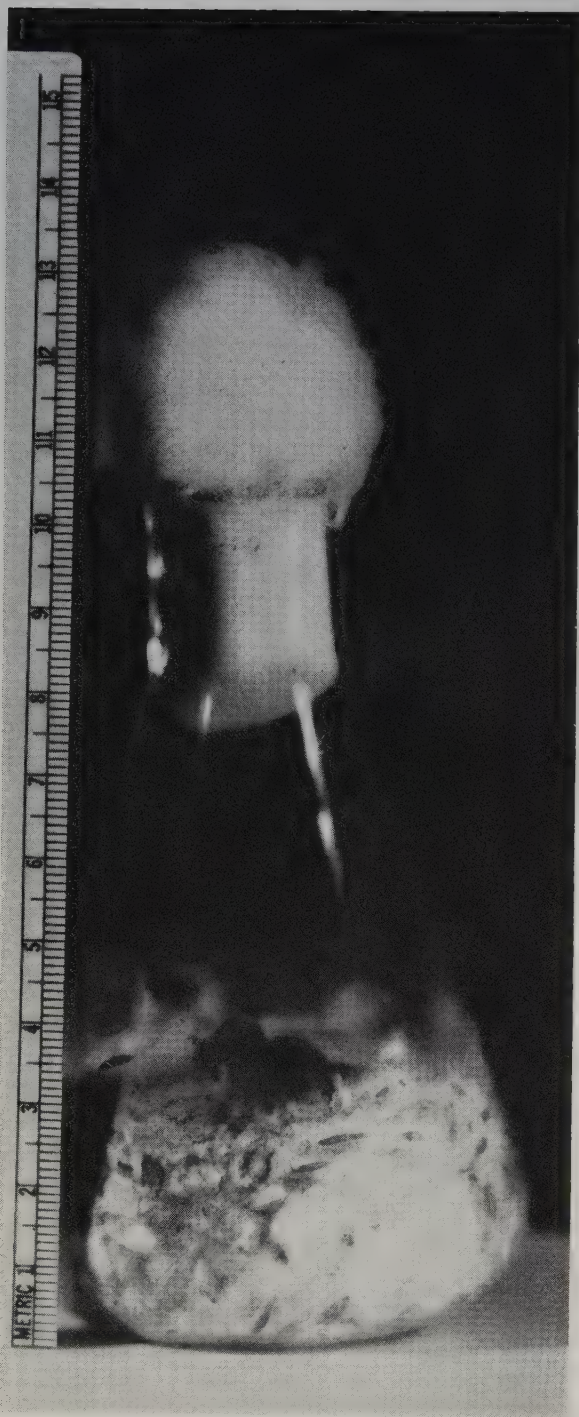


FIG. 167. An Erlenmeyer 125 ml. flask of sterile oats containing a culture of the fungus grown by *Myrmecocrypta ednaella* Mann that was developing an incipient sporophore on March 23, 1960. Its black cap or pileus was 16 mm. in maximum diameter and had a stalk 5.2 mm. long. It did not mature sufficiently for specific determination.

#### THE FUNGUS OF *APTEROSTIGMA* MAYRI

The garden of *Apterostigma* is commonly surrounded by a thin veil of the fungus. This veil is a natural extension of the hyphae that covers the substrate. Staphylae of ordinary forms are not formed. Terminal parts of hyphae, however, may be slightly and irregularly swollen in clavate form and clamp connections occur.

Contrary to earlier accounts in the literature, the veil surrounding the entire garden is not a production of the ants but is a natural growth of the fungus itself (Weber, 1946). In artificial cultures on hay in large flasks the hyphae would grow directly out at right angles to the grass stem, then form a continuous veil as a cylindrical wall outside the stem but separated from it by a sparse development of thin hyphae. The veil would collapse at the slightest touch.

Artificial cultures of the fungus were made to 2 per cent agar and to Sabouraud's dextrose agar the day an ant nest was taken in December, 1957, in Panama and transfers later made from them. Four days after a transfer made on January 16, there was a slowly growing dense mycelium. This culture was used to inoculate hay-agar, potato dextrose agar, oat and wheat flasks. During the remainder of 1958 the various cultures grew slowly except that an oat flask suddenly produced an apparent incipient sporophore in December. The mycologist Dr. L. Batra drew up a description of it on January 8, 1959. It was then mailed to a colleague who reported that it appeared to be an *Auricularia*. Unfortunately it did not mature further.

#### THE FUNGUS OF *MYRMECOCRYPTA* EDNAELLA

Cultures from a fungus garden of *Myrmecocrypta ednaella* Mann, taken in Panama on December 22, 1957, were obtained on Sabouraud's dextrose agar the same day. The garden at the time of collection consisted of a heterogeneous, woody substrate with an extremely scanty mycelium dotted with unusually compact staphylae. They were somewhat intermediate between the bromatia of *Cyphomyrmex rimosus* and the staphylae of higher attines. The staphylae were used as inocula and sprouted hyphae like those of higher attines. Transfers of these cultures showed a dense white mycelium of extremely fine hyphae. On October 9, 1959, flasks of oats and of wheat were inoculated with the mycelium of a nutrient agar tube of the



previous February 2. The mycelium consisted of short, densely growing hyphae.

Half of the flasks were kept in a darkened cabinet at 20.5°–28° C and half of the flasks were kept on a table in another room under a north window where it was 10°–15° C at night and close to 20° in the day.

One of the oat flasks of October 9 that was kept in the cooler room with fluctuating temperatures remained here until March 8 (fig. 167). It was then placed in the warmer room and started development of a sporophore later in the month. This sporophore ceased growth by April 4, 1960, and was removed when the pileus was 16 mm. in diameter and the stipe 9 mm. long. It was sent to an agaric specialist after being dried by air but was not fully mature and could not be identified.

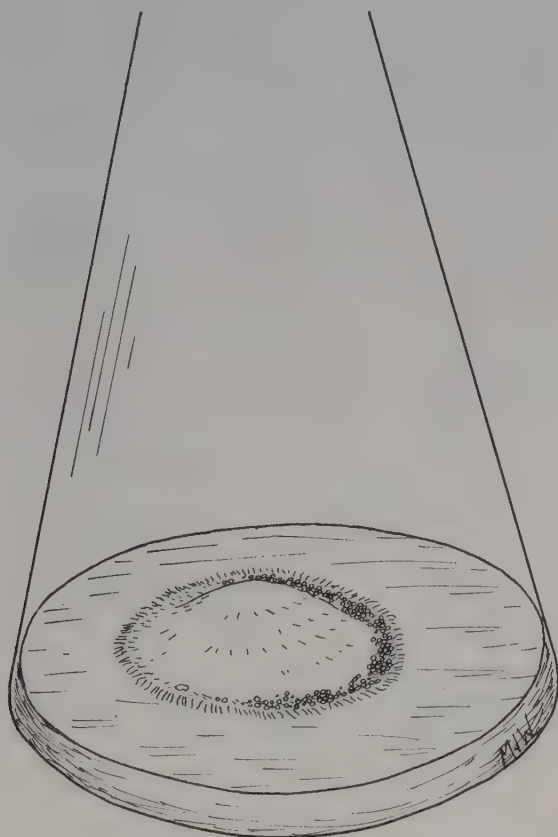


FIG. 168. Erlenmeyer 300 ml. flask of potato dextrose nutrient agar with a culture, several months old, of the fungus grown by *Sericomyrmex amabilis* Wheeler. The thick mycelial mass is raised and has staphylae (tiny circles) at the margin.



FIG. 169. Erlenmeyer 500 ml. flask of sterile oats with a culture, several months old, of the fungus grown by *Sericomyrmex amabilis* Wheeler. In this case the mycelium is scattered, as are the staphylae (tiny circles).

#### THE FUNGUS OF HIGHER ATTINES

Cultures of the fungi of *Sericomyrmex*, *Trachymyrmex*, *Acromyrmex*, and *Atta* sometimes developed massive growths that were dense and white in appearance. These grew on various media but did not develop further. As an example, *Sericomyrmex amabilis* fungus might grow in a compact mass, raised in the center, on potato dextrose agar (fig. 168) but as scattered islands (fig. 169) on oats. In both cases staphylae grew on the periphery.

#### EFFECT OF THE ANT FUNGUS ON OTHER ORGANISMS

Cultures of ant fungi were submitted for analysis to a commercial laboratory in 1955. They were tested for their possible effect on several harmful viruses and fungi as follows:

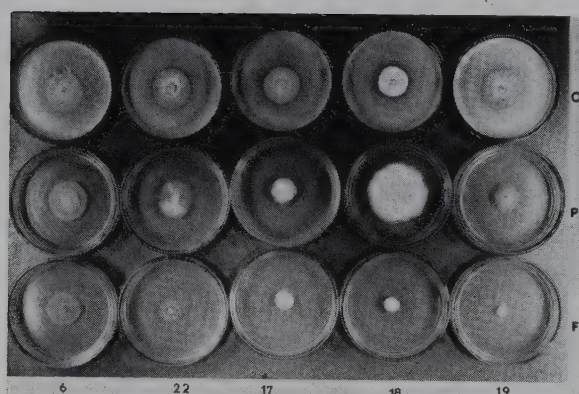


FIG. 170. Cultures of 5 ant fungi on 3 sets of agar plates as follows: row O = oatmeal agar; row P = potato dextrose; row F = Fries agar.

The fungi came from the following ants: W 19—*Cyphomyrmex costatus* Mann (col. 4475); W 18—*Cyphomyrmex costatus* Mann (col. 4472); W 17—*Cyphomyrmex costatus* Mann (col. 4471); W 22—*Apterostigma auriculatum* Wheeler (col. 4529); W 6—*Myrmicocrypta buenzlii* Borgmeier (col. 4330). From the New York Botanical Garden, Courtesy of W. J. Robbins and C. Rogerson.

The fungus of *Trachymyrmex septentrionalis* in extract proved active against several plant pathogens. Extracts were sprayed on tomato plants infected with *Fusarium* (a wilt disease) and on *Alternaria* (a leaf-spot disease) with some inhibitory effects on both.

The fungus of *Trachymyrmex bugnioni* and of *T. zeteki* in extract showed an inhibitory effect on the Southern bean mosaic virus.

The fungus of *Atta colombica tonsipes* showed an inhibitory effect on Newcastle disease virus in tissue culture of chick embryo cells.

My early speculations on possible antibiotic effects of the excretions of the ant fungi and ants (e.g., Weber, 1947, 1954, 1955a, c) led to testing these theories by other investigators.

I had long thought that possibly the ant saliva (and of course the anal deposits) were growth-promoting and investigations of such qualities have been difficult (e.g., Weber, 1955c). It is one thing to watch the ants apply saliva to the fungus and the skin of their brood and another matter to secure saliva in large enough quantity to analyze. In a 1956 trial I squeezed the ant heads slightly and applied the contents to agar plates streaked with the standard test organisms of the bacteriologists, *Staphylococcus aureus*, *Escherichia coli*, etc. I also tested ground fungus gardens and surrounding soil. There was no particular inhibition of the test organisms.

Martin, MacConnell, and Gale (1969) tested the antibiotic activity of *Atta colombica tonsipes* ants, their fungus, natural gardens, and exhausted substrate against standard test organisms and found no appreciable activity.

Suter (1954), in unsuccessfully attempting to find antibiotics in the fungus of the Trinidad *Atta cephalotes*, showed that the gardens, leaf sections, and the bodies of the workers carried bacteria and soil fungi. The ant fungus in culture inhibited the growth of *Serratia marcescens*.

#### THE PIONEER WORK OF ALFRED MOELLER

Alfred Moeller is the pioneer in mycological investigations on these ant fungi. He was trained in Germany under Professor Brefeld, an outstanding mycologist, and received a grant of 3,000 marks in 1890–1891 from the Berlin Academy of Science to travel to Brazil to study the ant fungus association. He went to Blumenau (27° S. Lat.) and set up his laboratory here. He then corresponded with the Swiss myrmecologist, Auguste Forel, and received identifications of the ants with which he was working.

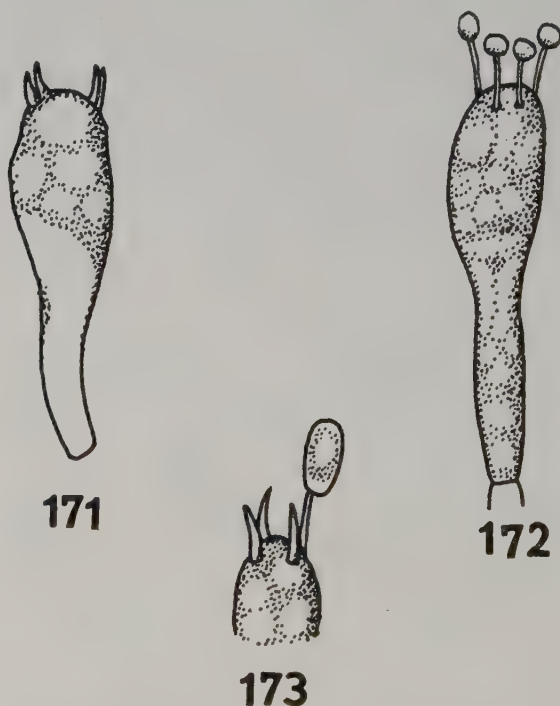
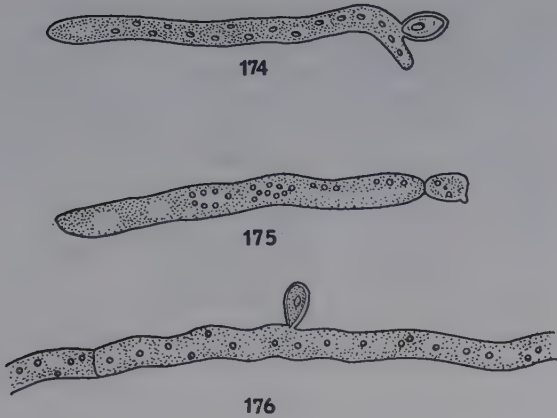


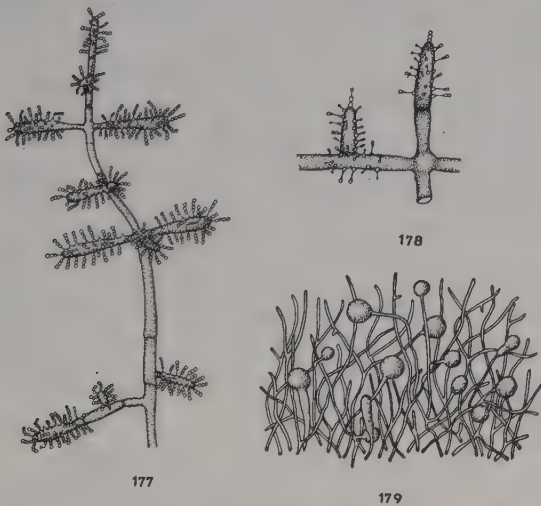
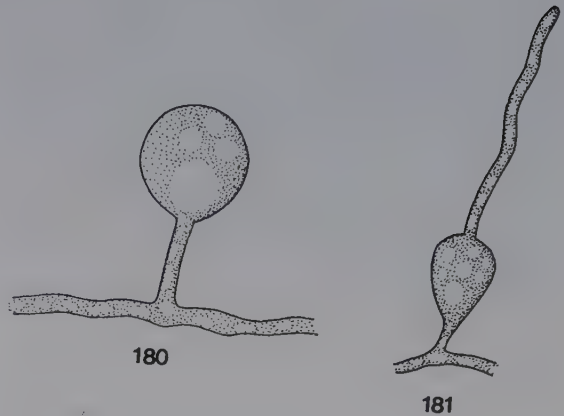
FIG. 171–173. The first scientific study of ant fungi, Moeller's 1893 report. Basidia of *Rozites gongylophora* from *Acromyrmex*.





FIGS. 174-176. Three germinating spores of the same.

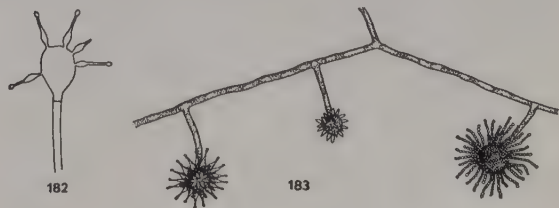
Field work began at the end of 1890 and concluded the following year. Some 10 representative species of ants and their gardens from *Cyphomyrmex* to *Acromyrmex* were studied, including four species of the latter genus. He did not appear to have examined *Atta* in the modern sense and therefore did not report on the really big *Atta* colonies. The four species of *Apterostigma* that were included suggest that the region was humid and well forested. Nearly eighty years later I visited nearby Rio Grande do Sul and was impressed by the exuberance and ubiquity of the attine fauna. It is hard to imagine a more suitable general area for these studies.

FIGS. 177-178. Two drawings of the conidial form of the strong *Acromyrmex* (=“*Atta*”) fungus, the smaller being a younger stage.FIG. 179. Hyphae in culture starting to form a staphyla or kohlrabi, from the fungus of *Acromyrmex*.FIGS. 180-181. Two single gongylidia or hyphal heads from the cultured fungus of *Acromyrmex*, one starting to send out a hypha (after Moeller).

The most abundant *Acromyrmex* near his laboratory was *discigera* and it is from the fungus of this ant that definitive stages were reared and to which the name *Rozites gongylophora* clearly applies (figs. 171-181). His technique was to transfer gardens to clean glass plates surrounded by petroleum moats and pick off the ants, one by one with forceps. Then parts of the garden were removed to watch glasses by as sterile means as possible.

The gongylidia commonly lost their contents to unexpanded hyphae within three days and conidia started to develop. The conidiophores were about  $8\mu$  long, and the spores  $2\mu$  in diameter (figs. 177-178). The mass breaks down on the fifth day. He felt that this conidial form was a development of the fungus of all four *Acromyrmex* species.

A second form of conidiophores which he called the weaker as contrasted with the stronger form was later grown. The ants in both cases tried desperately to cut and remove the abnormal growth. Although he never observed the act, he felt strongly that the aerial hyphae, from

FIGS. 182-183. Two drawings of the conidial form of the fungus of *Apterostigma*, one being a small, unripe head (after Moeller).

which conidia form, were bitten off by the ants. His graphic description of the frantic attempts to escape the growing conidial form have often been verified in my laboratory although he did not consider possible inhibitory effect of ant deposits.

Bacterial decomposition of the garden was believed to take place in the older parts of the garden during the winter.

Moeller gives the first detailed description of the staphylae ("Kohlrabi") growing in the garden and in artificial culture (fig. 179). The heads or gongylidia were never found to be separated by a dividing wall from the general course of the hypha. He had great success using these staphylae as inoculae for his cultures as was my experience years later. New gongylidia formed in artificial culture, a statement that was misunderstood by subsequent writers who said that these were found only in the ant garden.

He concluded that no conidial form would develop under the normal influence of the ants. Two different conidial forms appear when the ants are removed.

#### HIS DISCOVERY OF THE SPOROPHORES OF A FUNGUS

A man reported to him that he had found a large mushroom growth firmly united with an ant garden. A similar growth was found on a nest of *Acromyrmex discigera* (called here *Atta discigera*). Two similar growths were later seen in the same area and Moeller observed that two of these were slowly developing into mushrooms or sporophores. One of them took 10–12 days to mature. The mushrooms were as much as 16 cm. in diameter and were wine-red in color in the mature condition. The basidia were about 30  $\mu$  long and clavate (figs. 171–173). The four short sterigmata were 8  $\mu$  long. Spores were oval and ochre-colored (figs. 174–176).

Moeller then traced hyphae from the intact garden into the base of the mushroom and made detailed microscopic examinations. Other tests included an odor test: broken mushroom fragments left on the ground produced a strong, offensive odor reminiscent of malt, like the odor from a garden fragment that has been bottled tightly for two or three days. Ripe mushroom spores were germinated in nutrient solutions. Those few that germinated produced hyphae on the ninth day that were 10  $\mu$  thick and had side branches of 3  $\mu$ . Similar developments occurred in garden fungus cultures. In 5 weeks

the mycelium produced from spores formed the staphyla type of aggregates.

Similar results were obtained by culturing small fragments of the mushroom cap (pileus). These, too, formed the same type of staphylae as in the garden. Conidial forms could be grown like those above described. He found that the ants would accept the staphylae so produced as well as their own. They would also eat fragments of the mushrooms.

Moeller was somewhat reluctant to give a name to this ant fungus because of his limited library facilities but did name it *Rozites gonglyophora*. (The derivation of this word, which was not given by Moeller, is from the Greek for turnip.) He did say, however, that "I do not know for sure if the mushroom has not been described somewhere before" and this may be prophetic.

#### RE-EXAMINATION OF MOELLER'S WORK

Moeller's work long was accepted as definitive. Wheeler in 1907 referred to lacunae in these studies (as did Bequaert, 1922) and this appeared to be confirmed by my later translations of several statements of Moeller. Stahel and Geijskes reported in 1942 that their own studies in Surinam on *Atta cephalotes* and *sexdens* nests and ant fungi tended to confirm Moeller. They found three typical fruiting bodies in culture gardens of *cephalotes* that were covered with rough scales and resembled Moeller's *Rozites* but without inner differentiation in stipe and pileus.

Later they found a damaged sporophore growing from an *Atta cephalotes* nest and took parts of the pileus and stipe for cultures. Kohlrabi (staphylae) developed after the first 10 days and they felt that this sporophore fungus was truly the nest fungus of *Atta cephalotes*. They believed that the *cephalotes* fungus belonged to *Rozites gonglyophora* or at least was closely related to it. They could not find sporophores again in the 15 *Atta* nests that they examined. No sporophores developed from the mycelium of pure cultures.

#### *Conidial Forms of the Ant Fungus*

The fungus gardens may rarely develop conidia in a part of the garden that is relatively unattended.

Stahel and Geijskes (1941) brought portions of a colony and garden to the laboratory and



sometimes found that the formerly busy workers, attempting to rebuild the garden, would suddenly stop work. They would stand inert on the walls of the container and abandon the garden. The whole top part of the garden would then develop a white mold. After two days a high, snowy down of mycelium may form and a day later everything may be covered by a mass of brown conidia. The garden, in the meanwhile, shrinks badly. My experience has been similar with *Trachymyrmex*, *Acromyrmex* and *Atta* gardens in a few cases. However, from such cultures from gardens of *Acromyrmex* and *Atta* I have twice received tentative identifications of an unusual *Aspergillus* species so that caution is indicated in interpreting these developments as being those from *Rozites*.

#### EVOLUTION OF FUNGUS-GROWING

The stages in the evolution of the fungus-growing habit may have been:

Ants deposited their waste at particular sites in or near the nest.

Fungi developed on this, some being cellulose-digesting.

The biochemical qualities restricted the variety of fungi.

Certain fungi luxuriated as mycelial growths under these circumstances as the fungi become dependent on the ant deposits.

The adult ants cropped these fungi for food and fed hyphae to the larvae.

The ants added other insect droppings and

later vegetal debris as substrate, creating a fungus-garden.

A vigorous culture of the one fungus was maintained as the feces and saliva contributed nutrients that favored this fungus.

Chambers were excavated in the soil in which the brood and garden were kept.

When females left the parental nest they carried pieces of the hyphae, either between the mandibles or in the infrabuccal pocket off the pharynx.

These fragments of hyphae were deposited in a preformed cavity or later in the cell excavated by the female.

The female defecated on these, starting a new cycle of fungus culture.

Substrate was added, the luxuriating fungus was fed to the developing brood and a new colony was well launched.

Green leaves and fresh flowers were cut and used for substrate; the mycelium was planted.

The inexhaustible substrate and efficient culturing of the fungus permitted very large colonies with polymorphic workers to be developed.

In relation to these stages, the behavior of other ants might seem to be relevant, such as the harvesters that collect seeds and other vegetal material. No other ants, however, appear to show any early stages in fungus culture. A common harvester, *Pheidole*, does resemble the attine ants and further study may show a relationship.

## 9. GUESTS, PARASITES AND PREDATORS

### GUESTS AND PARASITES

The highly structured nests and colonies of the gardening ants contain other animals living in varied relations with the ants. The mutualistic relation that the ants have with their fungi involves actual metabolic reactions, as do parasitic relations. In parasitism, however, the parasite receives all or the greater part of the benefit of the association. Any animal that is first discovered in association with gardening ants may be classified simply as a "guest" until further study shows its relationship to be something different. Guests, or inquilines, usually do not have any effect on the metabolic activities of the ants. This is generally true of phoresis also, where the animal rides on the ant. These categories are man-made and in actuality an

animal may have a mixture of relations, as a mite riding on an ant but feeding on secretions at the ant's mouthparts.

Casual visitors include such animals as spiders that make temporary use of tunnels in *Atta* nests. More regular guests include a variety of beetles, crickets, and insects that live elsewhere but are attracted by the organic food, especially exhausted substrate, from the fungus gardens. Many other small animals, including worms, arachnids, and many insects, are found in this organic matter and can always be taken in variety in the waste chambers. Some of these may be restricted to this habitat. Lenko (1968) lists species of 13 arthropod orders taken in one *Acromyrmex* nest.

The appendix contains a list of animals associated with the attines.

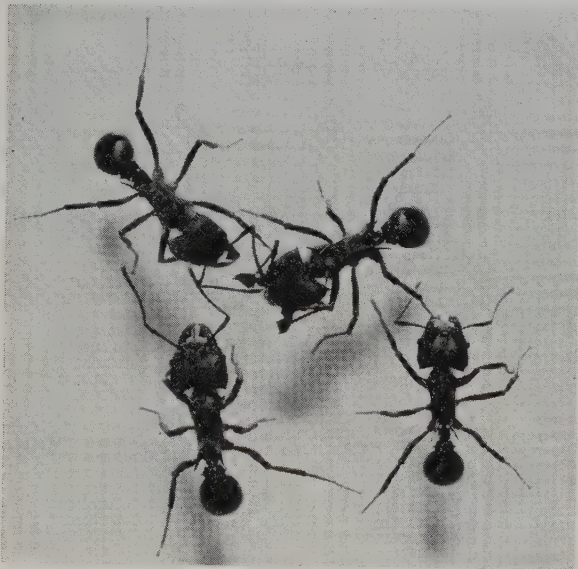


FIG. 184. Four living workers of the Argentine *Acromyrmex* (*Moellerius*) *striatus* Roger showing characteristic poses. One ant with mandibles widespread faces two others in a distress pose. Its other mouthparts are retracted. The ant closest to it is holding the apices of the antennae close to the mouthparts. Two ants are standing with antennae held parallel and in the act of rotating. The fore legs of all are held in a forward position, the hind legs are directed backwards and the middle pair are mostly forward. From a photograph taken by Richard E. Hewitt, Carnegie Institution of Washington, courtesy of C. P. Haskins.

### MITES

Most species of ants have mites on their bodies, and the attines are no exception. The most common types on attines are flattened, resemble a mud turtle, and cling securely to the legs. These mites are usually hypopial stages, nonfeeding nymphs, of Acaridae or related families of sarcoptiform mites. In healthy colonies these mites do not occur in large numbers, and the ants ignore the mites on their bodies. Whenever a colony is stagnant or deteriorating, however, mites soon multiply, infest the garden and may attach themselves to many workers. A spectacular example of an *Atta* with the front of the head almost covered by unidentified nymphal mites (hypopi) is shown (fig. 185). This ant was part of a deteriorating colony with a run-down garden.

A mite, *Tyrophagus brauni*, was apparently associated with a series of ant colonies of *Cyphomyrmex*, *Mycocepurus*, and *Apterostigma*. The ants were slow-moving and had small nests in soil or rotted wood. Nests of the three genera may occupy the same area of a few square decimeters, and there should be no difficulty in the mites transferring from one species to another. These tiny mites run over the integument of the ants and the mouthparts especially, where they may feed on fungus juices or saliva.



Since the ants were only 1.8 mm. in length the mites themselves were seen only under the microscope. The mites were seen to transfer quickly from one ant to another, as did *Garmania* on *Trachymyrmex septentrionalis*, and the latter genus of mite crawled from a worker to an ant larva. Another mite, probably *Garmania*, was seen transferring between two workers of *Cyphomyrmex rimosus* (fig. 186). The mite had been riding on the gaster of one ant when another brushed by, waving its antennae over the other ant as is customary (e.g., fig. 184).

In a flash the mite grabbed the left antennal tip, taking a position with its head facing proximally, and held tightly. The ant did not attempt to dislodge the mite and had already two others, one on the thorax, the other on the gaster. The mite on the antenna grasped firmly with all legs and kept its palpi appressed as the ant attempted to force its way through a narrow passageway, antennae probing the meanwhile. The mite had a rough ride but was not dislodged (Weber, 1955c).

A mite,? *Garmania*, was watched for more than ten minutes as it fed on a bromatium of *Cyphomyrmex rimosus*. It fed from below only, "pecking" at the fungus repeatedly and clearly ingesting it. The palps played continually over it. Some mites had their short mouthparts, in addition to the lateral palpi, appressed to the integument of the ants and may have been ingesting the epidermal secretions.

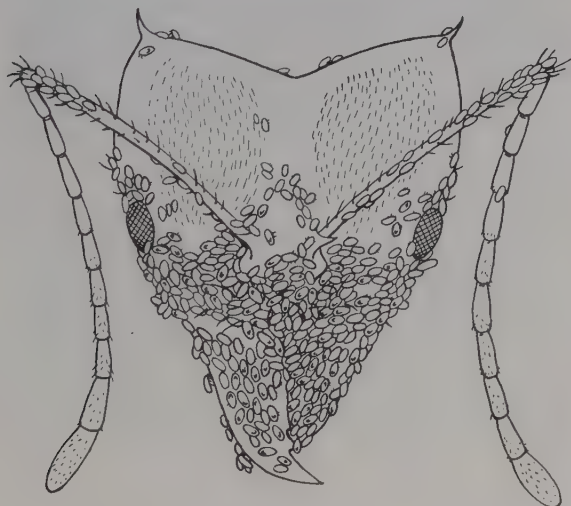


FIG. 185. A severe mite infestation on the head of a large worker of *Atta cephalotes isthmicola*. Mites increase greatly in numbers in deteriorating ant colonies.

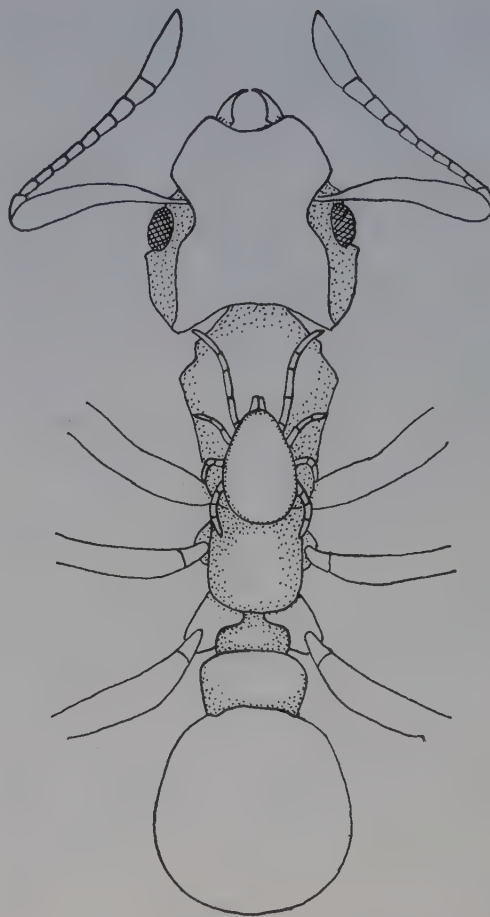


FIG. 186. A mesostigmatid mite in phoresy on the thorax of a worker of *Cyphomyrmex rimosus*. Such mites readily shift their position on the ants and ride in different places. They may take a position on the underside and feed on the fungus when the ant feeds. Florida. Drawn from life.

#### COLLEMBOLA

Collembola or springtails are conspicuous inhabitants of laboratory nests and regularly occur in nature about the fungus gardens. They tend to be more obvious in the laboratory because of better visibility in the plastic observation nests.

They may be seen feeding on the fungus, and the ants commonly try to bite them. The association confers nothing of value to the ants. They are harmful because of the fungus and substrate that they consume and their added wastes.

Usually Collembola frequent the soil on the periphery of the garden and have to cross a clear space, created by the ants, in order to

reach the fungus garden. They run quickly to the garden and dart in and out of its cavities wherever the ants are not active. When the ants do find them, the ants will dart quickly in their direction, with mandibles widespread, but captures are doubtless few. The Collembola have merely to release their spring and be propelled out of reach if they do not choose to run.

Panamanian nests of the same three *Cyphomyrmex*, *Mycocepurus*, and *Apterostigma* that had the *Tyrophagus* mite were infested by *Cyphoderus inaequalis*.

#### NEMATODE WORMS

The third class of social parasites of general distribution in the nests, besides the mites and Collembola, is nematode worms. These are often only 1.0–2.0 mm. long and are white or colorless. They infest the substrate in observation nests and one kind in a *Trachymyrmex zeteki* nest appeared to be a *Rhabditis* that was specialized for this existence by having a lower than normal reproductive capacity, the worms living in a relatively safe and secure environment (Weber, 1964). One is sure to find nematodes in great numbers in the substrate or cast-out material of any stagnant nest. The clear space created by the ants around the gardens makes it difficult for the worms and other inquilines to get into the gardens. The nematodes include true internal parasites such as one recorded from *Acromyrmex*.

The nematode, *Diploscapter lycosoma*, occurred in the pharyngeal glands of another ant (Markin and McCoy, 1968), and this occurrence suggests that they might be present in similar glands in attines where they could be transferred to other ants or the gardens.

#### PHORIDAE

Aggressive behavior is shown against the small endo-parasitic flies of the family Phoridae. It is a dramatic sight to see an ant react when a fly hovers over it, preparatory to ovipositing on the ant. In anthropomorphic terms, the ants act deathly afraid. An ant will rear up on its middle and hind legs, face the hovering fly with mandibles outspread, and wave the antennae. The fly sooner or later will dart down, whereupon the ant will maneuver to face it. The ant quickly turns around if the fly aims at the gaster. In most cases the fly darts down and tries to

oviposit at the base of the head, where the hatching larva can enter the body at the thin membrane of the neck. When a fly does succeed in lightly touching the back of an ant head, the ant rears up suddenly with the head turned back over the thorax. In doing this the ant may lose its grip on the clay slopes of the nest and tumble down. *Atta cephalotes* was parasitized by phorids of several sizes in Trinidad. The large ones tend to attack the soldiers, the small ones the smaller worker ants.

#### ANTS AS SOCIAL PARASITES OF ATTINES

The social parasite of *Acromyrmex*, *Pseudoatta*, has been described in chapter 3 under its own heading since it is also an attine but lacks the worker caste. Two other examples, however, differ in that they do not belong to this tribe and consist of complete colonies. Their very existence is a tribute to the successful colonies of attines.

Wheeler (1925) described *Megalomyrmex* (*Cepobroticus*) *symmetochus* from colonies of *Sericomyrmex amabilis* in Panama. The parasite queen usually took up her station in one of the cells of the host ant garden only one or two centimeters away from the host queen. The parasitic brood was kept in small clusters scattered through the garden and each cluster was cared for by a few workers. Although the adult ants and the broods of both species were thus intermingled, the workers of each species took care exclusively of their own brood and were never seen to transport the progeny of the other ant. The parasites fed upon the fungus of the host. This association was rediscovered in Panama in 1938 (Weber, 1941). In collecting one of the mixed colonies I found that the broods and workers of the two species were thoroughly intermingled but no hostility was shown as they separated their broods. Three host workers were seen in a cell licking the guest larvae and pupae, contrary to Wheeler's findings. These are easily distinguished from host broods by entirely different contours and hairs of the body. When a fragment of the garden of another attine, *Myrmicocrypta ednaella*, was placed next to the garden of the *Sericomyrmex*, the latter workers dismembered it and discarded the fragments. The *Megalomyrmex* workers came up and explored the pieces but did not feed on the fungus and took no part in the removal; apparently they were conditioned only to the *Sericomyrmex* fungus.



*Megalomyrmex wheeleri* was described from Panamanian nests of *Cyphomyrmex costatus* (Weber, 1940, 1941). This parasite, while smaller than *M. symmetochus*, was slightly larger than its host. Four mixed colonies were taken; two contained guest females only, which were quicker in their movements than their hosts. In one case the host garden was  $30 \times 20$  mm., and the chamber with the parasite had its only opening against this. In a second record the guest colony outnumbered the hosts and contained three dealated females. Their nest was less than 10 mm. from the host garden. When the nest was exposed the guests milled about instead of scattering as in nonparasitic species.

In general, investigators in the exuberant Neotropical fauna have not made the same detailed search for social parasites that myrmecologists have made in Europe and quite possibly more parasitic ants will be found to have adapted to the successful attines.

#### TERMITE-ATTINE RELATIONSHIPS

Both the termites and the gardening ants in the New World reduce the cellulose content of vegetation, the termites through their symbiotic protozoa, the ants through the action of their fungi. However, competition between the two groups of insects in the Neotropics is un-



FIG. 187. A young *Myrmecophaga jubatum* or giant anteater on the seawall in Guyana. A common habitat of this mammal is the Rupununi area of Guyana where *Atta sexdens*, *cephalotes* and *laevigata* and *Acromyrmex* (*M.*) *landolti* (*balzani* of authors) all occur and could be preyed upon.



FIG. 188. A Trinidad captive *Tamandua longicauda* anteater. This mammal is known to prey upon the two large leaf-cutters here, *Atta cephalotes* and *Acromyrmex octospinosus*.

important because one takes mostly fallen or dead vegetation, the other green leaves.

A different relation illustrated by Eidmann (1938) is that of *Acromyrmex* nesting inside and at the base of a termite (*Cornitermes*) carton nest surrounding the base of a plant and partly embedded in the ground. This association may be common and not entirely due to chance. The advantage to the ants of such a site was the impervious roof to the nest. The populous, spiny and active ants may have given the termite nest some protection from predators. This type of relationship was also seen in south Brazil (Weber, unpubl.) and included a third social insect colony, the notorious fire ant, *Solenopsis saevissima*. The latter ant may have fed on the termites. These fierce ants, however, may have given protection to the entire communal structure. They nested at the base of the termite mound, which was mostly embedded in the soil, and surrounding the garden of *Acromyrmex* (fig. 105). A similar relationship in Africa is reported by Ernst (1960) between a host *Cubitermes* termite mound and fungus-growing termites (*Microtermes*).

#### PREDATORS

When winged male and female attines are emerging from the parental nests they are particularly susceptible to predators. Many *Acromyrmex lundii* in Buenos Aires were eaten by birds, in some cases the females lost their gasters while the smaller males were eaten





FIG. 189. The common giant or marine toad, *Bufo marinus*, so bloated with ants as to have difficulty in moving. Veranda of house in Trinidad during an evening rain. This toad feeds on all sizes of attine ants.

entire. Bonetto (1959) notes sexual forms of various species of *Acromyrmex* falling prey to the carnivorous ants, *Ectatomma opaciventre* and *Parectatomma*.

The fungus-growers lack the distinctive relations with birds that the army ants show with the ant thrushes (Formicariidae). The latter are commonly attracted to swarm raids of army ants and the hordes of insects that are started up by them. Dense files of *Atta* bearing conspicuous sails of leaves or bright flower petals do not appear to attract birds.

The army ants (*Eciton* and related genera) commonly prey on the brood of other ants, including attines. Often their files will pass those of *Atta* without hostility. A different relationship, however, is that reported by Kazan,

Naumann and Rettenmeyer (pers. commun. 1971) in Ecuador between *Eciton rapax* and *Atta*. The two species appeared to live together harmoniously. Kazan watched one *rapax* colony that lived at least 27 days in an *Atta* nest. Possibly the *rapax* made use of one or more large *Atta* chambers that were empty or partly filled with refuse.

Among the most regular predators on the workers are the amphibians (toads and frogs). The common giant toad (*Bufo marinus*) feeds on small as well as large species (fig. 189). The stomachs of 26 toads were examined in Trinidad and the contents identified (Weber, 1938c). Out of 35 ant species identified, 4 were common fungus-growers, including *Acromyrmex* and *Atta*. It seemed absurd that these very large toads should have fed on *Cyphomyrmex* with workers only 2 mm. long.

Gallardo (1951, 1954) found Argentine amphibians and reptiles regularly preying on or living in the nests of *Acromyrmex* in Argentina. On my first thrust with a spade into a thatch nest of *Acromyrmex lobicornis* in Patagonia I unearthed a snake that quickly started down into the deeper chambers. There was time only to jab at it and cut off the tail. A colleague identified it as a boa type, *Elapomorphus lemniscatus*. Snake eggs were taken several times in the gardens of *Atta colombica tonsipes* in Panama as though they were suitable brood sites.

Vaz-Ferreira *et al.* (1970) found that 78 out of 577 *Acromyrmex lobicornis*, *hispidus*, and *striatus* nests contained eggs of reptiles in Uruguay. These included seven species of snakes and one of lizards. The eggs were not attacked by the ants, which clean part of the shells and cover other parts of them with the garden or garden debris. The garden temperature of 25°–30° C and high humidity made the site an ideal incubator. When the reptiles hatched they were able to escape unharmed by



190



191



192

FIG. 190. Sketch of head of *Mycetarotes* worker to show generic characters.

FIG. 191. Circlet of spines on the thorax of *Mycocepurus*, a generic character.

FIG. 192. Sketch of head of *Mycetosoritis* worker to show generic characters.



means of the amniotic fluid encircling the head. The most common reptiles were the snakes *Philodryas patagoniensis*, *Liophis obtusus*, and *Micrurus frontalis*.

Information is also limited on the exact role of the armadillos, common and widespread mammals in South America. I have found them tunneling into a nest of *Atta laevigata* in Venezuela.

Quite the most noteworthy predators, however, are the highly specialized anteaters. These neotropical mammals have lost their teeth and are highly specialized to feed on ants and termites. They have powerful claws on the front feet to tear open the nests and an exceedingly long and sticky tongue coated with mucus

which traps the ants. The stomach of a silky anteater, *Tamandua longicauda*, was filled with *Acromyrmex octospinosus* ants and another had *Atta cephalotes* (Weber, 1945) (fig. 188).

A common habitat for the giant anteater, *Myrmecophaga jubatum* (fig. 187) is the Rupununi Savannas, Guyana, and the common social insects here were termites such as *Amitermes*, and leaf-cutting ants, especially *Atta cephalotes*, *sexdens*, and *laevigata*, and *Acromyrmex* (*Moel-lerius*) *landolti balzani*. A tame, half-grown anteater fed indiscriminately on termites and ants. This anteater may be presumed to feed on the common attines as well as termites but this presumption should be verified by stomach examination.

# APPENDIX

## 1. KEY TO THE GENERA OF ATTINE WORKERS

1. a. Gaster smooth or finely punctate..... 2 posteriorly, ants monomorphic and about 2-3 mm..... 8
- b. Gaster tuberculate or with coarse hairs..... 9 *Mycocepurus* (fig. 191)
2. a. Dorsal body hairs squamate or appressed..... 3
- b. Dorsal body hairs simple or lacking..... 5
3. a. Head with complete, divergent antennal scrobes..... 4
- Cyphomyrmex* (fig. 31)
- b. Head with short antennal scrobes and frontal lobes..... 4
4. a. Head and thorax with dorsal squamate hairs on tubercles, occipital area angular..... 4
- Myrmicocrypta* (fig. 18)..
- b. Head with dorsal appressed hairs and no tubercles, occipital area smooth and rounded, no clearly bordered antennal scrobe..... 4
- Mycetophylax* (fig. 32)
5. a. Antennal scrobes complete, sub-parallel, occiput and thorax spinose or tuberculate..... 4
- Mycetarotes* (fig. 190)
- b. Antennal scrobes less complete and frontal lobes short..... 6
6. a. Thorax dorsally without spines, occipital area smooth and rounded, abundant flexuous pilosity..... 6
- Apterostigma* (figs. 19, 33)
- b. Thorax dorsally with spines or tubercles..... 7
7. a. Thoracic spines in the form of a circlet, frontal carinae slightly diverging and weakening posteriorly, ants monomorphic and about 2-3 mm..... 8
- b. Thoracic spines not in the form of a circlet... 8
8. a. Head cordate and without occipital spines; no thoracic spines; abundant flexuous hairs on the body, including gaster; size usually 3-5 mm..... 8
- Sericomyrmex* (figs. 20, 34)
- b. At least the posterior occipital spines present; thorax with 3 pair spines, pilosity sparse; size 2-12 mm. or more, the maximum a soldier.... 8
- Atta* (figs. 12, 30)
9. a. Antennal scrobes complete to occiput, no tuberculate dorsal hairs..... 10
- Mycetosoritis* (fig. 192)
- b. Antennal scrobes shorter or with dorsal hairs on tubercles..... 10
10. a. Antennal scrobes longer, comparatively monomorphic..... 10
- Trachymyrmex* (fig. 35)
- b. Antennal scrobes shorter, strongly polymorphic *Acromyrmex* (figs. 38, 68, 69)
- Acromyrmex* subgenera:
1. Occipital lobes rounded, no supra-ocular spine or tubercle subg. *Moellerius* (fig. 37)
2. Occipital lobes angular, with supra-ocular spine or tubercle..... subg. *Acromyrmex* (fig. 38)

## 2. ATTINE SPECIES NORTH OF SOUTH AMERICA

Species	U. S.	Mex-ico	West Indies	Central America	Trinidad	Species	U. S.	Mex-ico	West Indies	Central America	Trinidad
<i>Cyphomyrmex cham- pioni</i> Forel				x		<i>Cyphomyrmex rimosus</i>					
<i>Cyphomyrmex costatus</i> Mann				x		subsp. <i>breviscapus</i> Weber				x	
<i>Cyphomyrmex dentatus</i> Forel		x				<i>Cyphomyrmex rimosus</i> subsp. <i>flavescens</i> Weber			x		
<i>Cyphomyrmex flavidus</i> Pergande		x				<i>Cyphomyrmex rimosus</i> subsp. <i>minutus</i> Mayr	x	x	x	x	x
<i>Cyphomyrmex foxi</i> André			x			<i>Cyphomyrmex rimosus</i> subsp. <i>trinitatis</i> Weber				x	x
<i>Cyphomyrmex hamu- latus</i> Weber				x		<i>Cyphomyrmex salvini</i> Forel				x	
<i>Cyphomyrmex longis- capus</i> Weber				x		<i>Cyphomyrmex wheeleri</i> Forel	x	x			
<i>Cyphomyrmex rimosus</i> Spinola	x	x	x	x	x	<i>Mycetosoritis hart- manni</i> Wheeler	x				
<i>Cyphomyrmex rimosus</i> subsp. <i>arnoldi</i> Aguayo			x			<i>Mycetophylax con- formis</i> (Mayr)			x		x
<i>Cyphomyrmex rimosus</i> subsp. <i>major</i> Forel				x		<i>Mycocepurus smithi</i> Forel			x	x	x



## 2. ATTINE SPECIES NORTH OF SOUTH AMERICA—Continued

Species	U. S.	Mex-ico	West Indies	Central America	Trinidad	Species	U. S.	Mex-ico	West Indies	Central America	Trinidad
<i>Mycocepurus tardus</i> Weber				x		<i>Trachymyrmex desertorum</i> Wheeler	x				
<i>Myrmicocrypta buen-zlii</i> Borgmeier					x	<i>Trachymyrmex intermedius</i> Forel		x			
<i>Myrmicocrypta cucumis</i> (Mann)				x		<i>Trachymyrmex isthmicus</i> Santschi				x	
<i>Myrmicocrypta dilacerata</i> subsp. <i>cornuta</i> Forel				x		<i>Trachymyrmex jamaicensis</i> (André)			x		
<i>Myrmicocrypta ednaella</i> Mann				x		<i>Trachymyrmex jamaicensis</i> (André) subsp. <i>antiguensis</i> Weber			x		
<i>Myrmicocrypta godmani</i> Forel				x		<i>Trachymyrmex jamaicensis</i> (André) subsp. <i>cubaensis</i> Wheeler				x	
<i>Myrmicocrypta subnitida</i> Forel				x		<i>Trachymyrmex jamaicensis</i> (André) subsp. <i>frontalis</i> Santschi				x	
<i>Myrmicocrypta urichi</i> Weber					x	<i>Trachymyrmex jamaicensis</i> (André) subsp. <i>haytianus</i> Wheeler and Mann				x	
<i>Apterostigma auriculatum</i> Wheeler				x		<i>Trachymyrmex jamaicensis</i> (André) subsp. <i>sharpi</i> Forel				x	
<i>Apterostigma auriculatum</i> subsp. <i>icta</i> Weber				x	x	<i>Trachymyrmex nogalensis</i> Byars	x				
<i>Apterostigma calverti</i> Wheeler				x		<i>Trachymyrmex opulenta</i> (Mann)				x	
<i>Apterostigma dentigerum</i> Wheeler				x		<i>Trachymyrmex relictus</i> Borgmeier					x
<i>Apterostigma ierense</i> Weber					x	<i>Trachymyrmex ruthae</i> Weber					x
<i>Apterostigma ierense</i> subsp. <i>fitzgeraldi</i> Weber					x	<i>Trachymyrmex saussurei</i> Forel		x			
<i>Apterostigma mayri</i> Forel				x	x	<i>Trachymyrmex septentrionalis</i> McCook	x				
<i>Apterostigma robustum</i> Emery				x		<i>Trachymyrmex squamulifer</i> Emery				x	
<i>Apterostigma tramitis</i> Weber				x		<i>Trachymyrmex smithi</i> Buren		x			
<i>Apterostigma urichi</i> Forel					x	<i>Trachymyrmex smithi</i> subsp. <i>neomexicanus</i> Cole	x				
<i>Apterostigma collare</i> Emery		x		x		<i>Trachymyrmex tur-rifex</i> Wheeler	x	x			
<i>Apterostigma scutellare</i> Forel		x				<i>Trachymyrmex urichi</i> Forel				x	x
<i>Sericomyrmex amabilis</i> Wheeler				x		<i>Trachymyrmex zeteki</i> Weber				x	
<i>Sericomyrmex aztecus</i> Forel		x				<i>Acromyrmex</i> (A.) <i>coronatus</i> Fabr. subsp. <i>angustata</i> Forel				x	
<i>Sericomyrmex urichi</i> Forel					x						
<i>Sericomyrmex zacapanus</i> Wheeler		x									
<i>Trachymyrmex arizonensis</i> Wheeler	x										
<i>Trachymyrmex bugnioni</i> Forel				x	x						
<i>Trachymyrmex cornetzi</i> Forel				x	x						

2. ATTINE SPECIES NORTH OF SOUTH AMERICA—*Continued*

Species	U. S.	Mex-ico	West Indies	Central America	Trinidad	Species	U. S.	Mex-ico	West Indies	Central America	Trinidad
<i>Acromyrmex</i> (A.) <i>coronatus</i> Fabr. subsp. <i>importunus</i> Santschi				x		<i>ekchuah</i> Wheeler				x	
<i>Acromyrmex</i> (A.) <i>coronatus</i> Fabr. subsp. <i>panamensis</i> Forel				x		<i>Acromyrmex</i> (A.) <i>octospinosus</i> subsp. <i>vulcanus</i> Wheeler				x	
<i>Acromyrmex</i> (A.) <i>coronatus</i> Fabr. subsp. <i>rectispina</i> Forel				x		<i>Acromyrmex</i> (Moel- lerius) <i>versicolor</i> Pergande	x	x			
<i>Acromyrmex</i> (A.) <i>octospinosus</i> (Reich)		x	x	x	x	<i>Acromyrmex</i> (Moel- lerius) <i>versicolor</i> subsp. <i>chisoensis</i> Wheeler	x				
<i>Acromyrmex</i> (A.) <i>octospinosus</i> subsp. <i>cubanus</i> Wheeler			x			<i>Atta cephalotes</i> (L)		x		x	x
<i>Acromyrmex</i> (A.) <i>octospinosus</i> subsp. <i>echinator</i> Forel				x		<i>Atta cephalotes</i> subsp. <i>lutea</i> Forel			x		
<i>Acromyrmex</i> (A.) <i>octospinosus</i> subsp.						<i>Atta colombica</i> <i>tonsipes</i> Santschi				x	
						<i>Atta insularis</i> Guerin			x		
						<i>Atta mexicana</i> (F. Smith)	x	x			
						<i>Atta sexdens</i> (L)				x	
						<i>Atta texana</i> (Buckley)	x				



## 3. MATING FLIGHTS OF ATTINES

## APPENDIX

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Species	Locality	Date	Time	Previous day	Temp. air -C	Temp. surface	Remarks	Source
<i>Trachymyrmex septentrionalis</i>	Mississippi	July-August	10:22 A.M.	124 mm. rain			see text	Cole, 1939
"	Florida	19.v.59	4:30 P.M.	124 mm. rain	32		newly descended female	Weber, unpubl.
"	"	19.vi.59		rain			male flying singly	"
"	"	24.vi.59	12:10-25 P.M.	clear	28.4		newly descended females	"
"	"	26.vi.59	8:40-9:10 A.M.	clear	25		females	"
"	"	29.vi.59	8 A.M.	clear	27.5	27.2	newly descended females	"
"	New Jersey	4.ix.56	3:12-3:24 P.M.		30.8	32	females took flight singly	"
"	Louisiana	4.vii.63	P.M. to 2:15	17 mm. rain	31.5		see text	Moser, pers. comm.
"	Argentina	17.xii.58	7-11 P.M.	clear			one female, two males	Kusnezov, 1962
"	Colombia	1.viii.38	3-4 A.M.	rain			to light	Weber, 1958
"	Trinidad	27.vi.64	9:30-10 A.M.	rain			newly descended sexes	Weber, unpubl.
"	"	1.vii.65	6:45-8:45 A.M.	40 mm. rain	28.2	31	"	"
"	"	25.iv.67	8 A.M.	heavy rain			flying and descending singly	Weber, 1967
<i>Acromyrmex (A.) lundii</i>	Uruguay	11.xii.61	early A.M.	rain			flight fell in Rio de la Plata	Weber, unpubl.
"	Argentina	18.x, 2.xi.18	A.M.				35 females isolated	Bruch, 1921
"	"	Sept.-Jan.	A.M.				copulation commences in air	Kusnezov, 1962
"	"	Oct.-Dec.		rain			copulate in air	Weber, unpubl.
"	"	2.xi.61	6:50-7:24 A.M.	clear, humid	21.7-22.2		end of flight	"
"	"	11.xi.61	10-10:55 A.M.	clear, humid	18.5		flight beside house	"
"	"	17.xii.61	11-11:50 A.M.	cool	22	22	see text	"
"	"	14.xi.61	7:10-7:40 A.M.	rain	19-20.5		full flight	"
"	"	Oct.-Nov. 38	7-10 A.M.	clear			16 females, 32 males	Goetsch, 1939
"	Trinidad	1.vii.65	7:30-10:45 A.M.	40 mm. rain	28	31	see text	Weber, unpubl.
"	Trinidad	27.vi.64	9:30-10 A.M.	rain			males fallen in gutter	Weber, unpubl.
"	"	1.vii.65	7:30-8 A.M.	40 mm. rain	28.2	31	sexes descending singly	Weber, 1967
"	"	9.vi.67	7:30-8:18 A.M.	heavy rain	26	27.5	male-female ratio: 100 to 1	" unpubl.
"	"	25.iv.67	8 A.M.	rain			first flight of year	Cherrett, unpubl.
<i>Acromyrmex (M.) versicolor</i>	Arizona	30.vii	5:50 A.M.	heavy rain			see text	Wheeler, 1917
<i>Atta capiguara</i>	Brazil	Sept.-Dec.	10 A.M.-6 P.M.	rain			see text	Amante, 1967b
"	Trinidad	11.vii.64	7:50 A.M.	clear			male in ditch	Weber, unpubl.
"	"	1.vii.65	A.M.				male taken on path	"
"	"	28.vi.65	8:30 A.M.				2 females flying to islet	"
"	"	9.vii.66						Cherrett, 1968

## 3. MATING FLIGHTS OF ATTINES—Continued

Species	Locality	Date	Time	Previous day	Temp. air -C	Temp. surface	Remarks	Source
<i>Atta cephalotes</i>	Surinam	Apr.-June					chief flight in May	Geijskes, 1953
" <i>laevigata</i>	Brazil	Sept.-Dec.	10 A.M.-6 P.M.				see text	Amante, 1967b
" <i>sexdens</i>	Surinam	Dec.-Feb.	3 P.M.				chief flight in Jan.	Geijskes, 1953
" "	Brazil	Sept.					fly from bushes	Autuori, 1947, 1956
" "	"	Sept.-Dec.	10 A.M.-4 P.M.			about 20		Amante, 1966
" <i>lexana</i>	Texas	May	9 P.M.				see text	Walter <i>et al.</i> , 1938
" "	Louisiana	Apr.-May	3:30-4:15 A.M.		16-25.5		see text	Moser, 1967
" <i>vollenweideri</i>	Argentina	Oct.-Jan.		rain				Goetsch, 1939
" "	"	Oct.-Jan.						Kusnezov, 1962



## 4. GUESTS, PARASITES AND PREDATORS OF ATTINES

Taxonomic group	Species	Attine	Relationship	Reference
Rotifera	rotifers	<i>Trachymyrmex zeteki</i>	in refuse	Weber, 1964
Nematoda	<i>Rhabditis</i> type	<i>Trachymyrmex zeteki</i>	in refuse	Weber, 1964
Nematoda	nematode	<i>Acromyrmex octospinosus</i>	parasites	Weber, 1945
Nematoda	nematode	<i>Cyphomyrmex costatus</i>	in garden	Weber, 1957
Annelida	<i>Pontoscolex corethrus</i>	<i>Atta sexdens</i>	in chamber	Eidmann, 1938
Annelida	oligochaete	<i>Trachymyrmex zeteki</i>	in refuse	Weber, 1964
Gastropoda	snail	<i>Cyphomyrmex costatus</i>	predator	Weber, 1957
Myriapoda	millipeds	<i>Cyphomyrmex costatus</i>	in nest	Weber, 1957
Chilopoda	centipede	<i>Acromyrmex lobicornis</i>	in nest	Weber, unpubl.
Pseudoscorpionida	pseudoscorpion	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Pseudoscorpionida	<i>Allochernes</i> n. sp.	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Isopoda	<i>Platyarthrus scoblii</i>	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Isopoda	sowbug	<i>Cyphomyrmex costatus</i>	in nest	Weber, 1957
Araneae	<i>Cesonia bilineata</i>	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Araneae	<i>Bothriocyrtum</i>	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Araneae	<i>Cicurina arcata</i>	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Araneae	<i>Crammonota pictilis</i>	<i>Atta texana</i>	in nest	Walter <i>et al.</i> , 1938
Araneae	tarantula	<i>Acromyrmex octospinosus</i>	in tunnel	Weber, 1945
Araneae	<i>Triaxeris patellaris</i>	<i>Cyphomyrmex costatus</i>	predator	Weber, 1957
Acarina	<i>Typhlotrombidium tridentifer</i>	<i>Atta texana</i>		Walter <i>et al.</i> , 1938
Acarina	<i>Tarsonemus</i>	<i>Atta texana</i>		Walter <i>et al.</i> , 1938
Acarina	<i>Macrocheles</i>	<i>Atta texana</i>		Walter <i>et al.</i> , 1938
Acarina	<i>Garmannia</i>	<i>Cyphomyrmex rimosus</i>	phoretic	Weber, 1955
Acarina	<i>Tyrophagus brauni</i>	<i>Cyphomyrmex costatus</i>	phoretic	Weber, unpubl.
Acarina	<i>Tyrophagus brauni</i>	<i>Mycocarpus tardus</i>	phoretic	Weber, unpubl.
Acarina	<i>Tyrophagus brauni</i>	<i>Apterostigma dentigerum</i>	phoretic	Weber, unpubl.
Acarina	<i>Ereynetes</i>	<i>Trachymyrmex septentrionalis</i>	phoretic	Weber, 1956
Acarina	<i>Garmannia</i> sp.	<i>Trachymyrmex septentrionalis</i>	phoretic	Weber, 1956
Acarina	<i>Oplitis</i> sp.	<i>Trachymyrmex septentrionalis</i>	phoretic	Weber, unpubl.
Acarina	<i>Tyrophagus</i>	<i>Trachymyrmex septentrionalis</i>	phoretic	Weber, unpubl.
Acarina	Acaridae hypopi	<i>Atta sexdens</i>	phoretic	Weber, unpubl.
Acarina	Acaridae hypopi	<i>Atta cephalotes</i>	phoretic	Weber, unpubl.
Acarina	<i>Hirstiostoma feroniarum</i>	<i>Atta cephalotes isthmicola</i>	phoretic	Weber, unpubl.
Acarina	<i>Scutacarus</i>	<i>Atta colombica tonsipes</i>	phoretic	Weber, unpubl.
Acarina	<i>Fuscuoropoda</i>	<i>Atta texana</i>	phoretic	Moser, 1967
Acarina	<i>Oplitis</i>	<i>Atta texana</i>	phoretic	Moser, 1967
Acarina	<i>Proctolaelaps</i>	<i>Atta texana</i>	phoretic	Moser, 1967
Diplura	<i>Metajapyx?</i>	<i>Atta texana</i>	in chamber	Moser, 1963
Thysanura	<i>Atelura</i>	<i>Atta texana</i>	in refuse	Walter <i>et al.</i> , 1938
Thysanura	<i>Grassiaella praestans</i>	<i>Atta texana</i>	in refuse	Eidmann, 1938
Thysanura	<i>Attatelura geijskesi</i>	<i>Atta sexdens</i>	in nest	Wygodzinsky, 1942
Thysanura	<i>Attatelura geijskesi</i>	<i>Atta cephalotes</i>	in nest	Wygodzinsky, 1942
Collembola	<i>Cyphoderus similis</i>	<i>Cyphomyrmex costatus</i>	fungus feeder	Weber, unpubl.
Collembola	<i>Cyphoderus similis</i>	<i>Apterostigma dentigerum</i>	fungus feeder	Weber, unpubl.
Collembola	<i>Cyphoderus inaequalis</i>	<i>Cyphomyrmex costatus</i>	fungus feeder	Weber, 1957
Collembola	<i>Cyphoderus inaequalis</i>	<i>Trachymyrmex cornetzi</i>	fungus feeder	Weber, unpubl.
Collembola	<i>Cyphoderus inaequalis</i>	<i>Trachymyrmex zeteki</i>	fungus feeder	Weber, 1964
Collembola	<i>Cyphoderus inaequalis</i>	<i>Apterostigma dentigerum</i>	fungus feeder	Weber, unpubl.
Collembola	<i>Cyphoderus inaequalis</i>	<i>Mycocarpus tardus</i>	fungus feeder	Weber, unpubl.
Collembola	<i>Pseudosira eidmanni</i>	<i>Atta sexdens</i>	in refuse	Eidmann, 1938
Collembola	<i>Pseudosinnela violenta</i>	<i>Atta texana</i>	in refuse	Walter <i>et al.</i> , 1938
Blattaria	<i>Arenivaga bolliana</i>	<i>Atta texana</i>	in refuse	Walter <i>et al.</i> , 1938
Blattaria	<i>Arenivaga tonkawa</i>	<i>Atta texana</i>	in refuse	Walter <i>et al.</i> , 1938
Blattaria	<i>Attaphila fungicola</i>	<i>Atta texana</i>	phoretic	Walter <i>et al.</i> , 1938
Blattaria	roach	<i>Atta cephalotes</i>	fungus feeder	Weber, 1945
Blattaria	<i>Myrmicophila nebrascensis</i>	<i>Atta cephalotes</i>	phoretic	Walter <i>et al.</i> , 1938
Blattaria	roach	<i>Acromyrmex hispidus</i>	fungus feeder	Weber, unpubl.
Blattaria	roach	<i>Apterostigma ierense</i>	fungus feeder	Weber, 1945
Corrodentia	psocids	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Lepidoptera	<i>Atticonviva</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938

4. GUESTS, PARASITES AND PREDATORS OF ATTINES—*Continued*

Taxonomic group	Species	Attine	Relationship	Reference
Hemiptera	<i>Tominotus unisetosus</i>	<i>Atta texana</i>	in chamber	Moser, 1963
Coleoptera	<i>Sarariphaeus luridipennis</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Coleoptera	<i>Lobopoda direaeoides</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Coleoptera	<i>Ontherus zikani</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Coleoptera	<i>Euphoria lurida?</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Coleoptera	<i>Oosternum attacomis</i>	<i>Atta texana</i>	in refuse	Spangler, 1962
Staphylinidae	Staphylinid	<i>Acromyrmex octospinosus</i>	in nest	Weber, 1945
Staphylinidae	<i>Gymnetis tigrina</i>	<i>Acromyrmex lobicornis</i>	predator	Bruch, 1917
Coleoptera	<i>Euparixia formica</i>	<i>Atta mexicana?</i>	in refuse	Woodruff & Cartwright, 1967
Coleoptera	<i>Euparixia bruneri</i>	<i>Atta insularis?</i>	in refuse	Woodruff & Cartwright, 1967
Coleoptera	<i>Euparixia moseri</i>	<i>Atta texana</i>	in refuse	Woodruff & Cartwright, 1967
Coleoptera	<i>Lobopoda subcuneata</i>	<i>Atta texana</i>	in refuse	Moser, 1963
Coleoptera	<i>Euparixia duncani</i>	<i>Acromyrmex (M.) versicolor?</i>	in refuse	Woodruff & Cartwright, 1967
Coleoptera	<i>Saprinus</i>	<i>Atta texana</i>	in refuse	Moser, 1963
Coleoptera	<i>Tachyura dolasa</i>	<i>Atta texana</i>	in refuse	Moser, 1963
Coleoptera	<i>Conoderus</i>	<i>Atta texana</i>	in refuse	Moser, 1963
Coleoptera	<i>Coelosia hippocrates</i>	<i>Atta vollenweideri</i>	in refuse	Bruch, 1917
Milichiidae	<i>Pholeomyia texensis</i>	<i>Atta texana</i>	in refuse	Sabrosky, 1959
Milichiidae	<i>Pholeomyia comans</i>	<i>Atta texana</i>	larvae in refuse	Moser, 1963
Milichiidae	<i>Pholeomyia decorior</i>	<i>Trachymyrmex septentrionalis</i>	following ant	Sabrosky, 1959
Phoridae	unidentified	<i>Atta cephalotes</i>	predator	Weber, 1945
Phoridae	<i>Allochaeta longiciliata</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1926
Phoridae	<i>Allochaeta propinqua</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1926
Phoridae	<i>Apocephalus atrophilus</i>	<i>Atta sexdens</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus</i> sp.	<i>Atta cephalotes</i>	predator	Eibl-Eibesfeldt, 1967
Phoridae	<i>Apocephalus rionegrensis</i>	<i>Acromyrmex subterraneus</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus dubitatus</i>	<i>Acromyrmex subterraneus</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus luteihalteratus</i>	<i>Acromyrmex lundii</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus neivai</i>	<i>Acromyrmex</i> sp.	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus barbicauda</i>	<i>Acromyrmex lundii</i>	predator	Borgmeier, 1931
Phoridae	<i>Apocephalus lamellatus</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius grandicornis</i>	<i>Atta sexdens</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius tursipennis</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius crudelis</i>	<i>Atta sexdens</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius catharinensis</i>	<i>Acromyrmex lundii</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius gracilipes</i>	<i>Acromyrmex subterraneus</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius cuspidatus</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius persecutor</i>	<i>Acromyrmex lundii</i>	predator	Borgmeier, 1931
Phoridae	<i>Myrmosicarius infestans</i>	<i>Acromyrmex subterraneus</i>	predator	Borgmeier, 1931
Phoridae	<i>Dohrniphora paraguayana</i>	<i>Atta sexdens</i>	predator	Borgmeier, 1960
Phoridae	<i>Neodohrniphora declinata</i>	<i>Atta laevigata</i>	predator	Borgmeier, 1931
Phoridae	<i>Neodohrniphora acromyrmecis</i>	<i>Acromyrmex</i> sp.	predator	Borgmeier, 1931
Phoridae	<i>Neodohrniphora wasmanni</i>	<i>Atta sexdens</i>	predator	Borgmeier, 1931
Phoridae	<i>Stenoneurellis laticeps</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Phoridae	<i>Procliniella hostilis</i>	<i>Acromyrmex muticinus</i>	predator	Borgmeier, 1931
Hymenoptera	<i>Trichopria</i>	<i>Trachymyrmex zeteki</i>	parasite?	Weber, 1964
Hymenoptera	<i>Galesus</i>	<i>Atta texana</i>	unclear	Walter <i>et al.</i> , 1938
Hymenoptera	<i>Scolia guttata</i>	<i>Atta texana</i>	unclear	Walter <i>et al.</i> , 1938
Formicidae	<i>Gnamptogenys hartmanni</i>	<i>Trachymyrmex septentrionalis</i>	predator	Echols, 1964
Formicidae	<i>Gnamptogenys turmalis</i>	<i>Trachymyrmex septentrionalis</i>	predator	Kempf & Brown, 1968
Formicidae	<i>Parectatomma</i>	<i>Acromyrmex</i> spp.	predator	Bonetto, 1959
Formicidae	<i>Ectatomma tuberculatum</i>	<i>Atta cephalotes</i>	predator	Weber, 1946a
Formicidae	<i>Ectatomma opaciventre</i>	<i>Atta vollenweideri</i>	predator	Bonetto, 1959
Formicidae	<i>Ectatomma ruidum</i>	<i>Acromyrmex octospinosus</i>	predator	Weber, 1946a



4. GUESTS, PARASITES AND PREDATORS OF ATTINES—*Continued*

Taxonomic group	Species	Attine	Relationship	Reference
Formicidae	<i>Ectatomma ruidum</i>	<i>Trachymyrmex urichi</i>	predator	Weber, 1946a
Formicidae	<i>Neivamyrmex fallax</i>	<i>Atta texana</i>	in chamber	Moser, 1963
Formicidae	<i>Neivamyrmex nigrescens</i>	<i>Trachymyrmex septentrionalis</i>	predator	Cole, 1939
Formicidae	<i>Nomamyrmex esenbecki</i>	<i>Atta laevigata</i>	predator	Borgmeier, 1955
Formicidae	<i>Nomamyrmex esenbecki</i>	<i>Atta mexicana</i>	predator	Borgmeier, 1955
Formicidae	<i>Nomamyrmex esenbecki</i>	<i>Acromyrmex rugosus</i>	predator	Borgmeier, 1955
Formicidae	<i>Nomamyrmex hartigi</i>	<i>Atta</i>	predator	Borgmeier, 1955
Formicidae	<i>Labidus</i> sp.	<i>Cyphomyrmex costatus</i>	predator	Weber, 1941
Formicidae	<i>Eciton schmitti</i>	<i>Trachymyrmex septentrionalis</i>	predator	Cole, 1939
Formicidae	<i>Eciton quadriglume</i>	<i>Atta</i>	predator	Reichensperger, 1924
Formicidae	<i>Eciton quadriglume</i>	<i>Acromyrmex</i>	predator	Borgmeier, 1955
Formicidae	<i>Eciton dulcius</i>	<i>Atta</i>	predator	Bruch, 1923
Formicidae	<i>Eciton dulcius</i>	<i>Acromyrmex heyeri</i>	occupied cells	Bruch, 1923
Formicidae	<i>Eciton dulcius</i>	<i>Acromyrmex silvestrii</i>	occupied cells	Bruch, 1923
Formicidae	<i>Carebarella bicolor</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Formicidae	<i>Erebomyrma eidmanni</i>	<i>Atta sexdens</i>	in nest	Eidmann, 1938
Formicidae	<i>Wasmannia auropunctata</i>	<i>Cyphomyrmex rimosus</i>	predator	Weber, 1955
Formicidae	<i>Deromyrma</i>	<i>Trachymyrmex cornetzi</i>	predator	Weber, 1941
Formicidae	<i>Megalomyrmex symmetochus</i>	<i>Sericomyrmex amabilis</i>	fungus feeder	Wheeler, 1925
Formicidae	<i>Megalomyrmex wheeleri</i>	<i>Cyphomyrmex costatus</i>	fungus feeder	Weber, 1940
Formicidae	<i>Pseudoatta argentina</i>	<i>Acromyrmex lundii</i>	social parasite	Gallardo, 1916
Anguillidae	<i>Symbranchus marmoratus</i>	<i>Atta cephalotes</i>	in nest	Stahel & Gajskes, 1936
Bufo	<i>Bufo marinus</i>	<i>Cyphomyrmex rimosus</i>	predator	Weber, 1938
Bufo	<i>Bufo marinus</i>	<i>Trachymyrmex urichi</i>	predator	Weber, 1938
Bufo	<i>Bufo marinus</i>	<i>Sericomyrmex urichi</i>	predator	Weber, 1945
Bufo	<i>Bufo marinus</i>	<i>Acromyrmex octospinosus</i>	predator	Weber, 1938
Bufo	<i>Bufo marinus</i>	<i>Atta sexdens</i>	predator	Weber, 1938
Bufo	<i>Bufo marinus</i>	<i>Atta cephalotes</i>	predator	Weber, 1945
Bufo	<i>Bufo granulosus fernandyci</i>	<i>Acromyrmex</i>	in chamber	Gallardo, 1964
Salientia	<i>Leptodactylus</i>	<i>Acromyrmex</i>	in chamber	Gallardo, 1964
Squamata	<i>Gymnophthalmus rubricauda</i>	<i>Acromyrmex lundii</i>	in chamber	Gallardo, 1951
Squamata	<i>Tupinambis teguixin</i>	<i>Atta sexdens</i>	eggs in nest	Eidmann, 1938
Squamata	<i>Amphisbaena</i>	<i>Atta cephalotes</i>	in nest	Weber, 1945
Squamata	<i>Amphisbaena alba</i>	<i>Atta cephalotes</i>	in chambers	Stahel & Geijskes, 1939
Squamata	<i>Basiliscus basiliscus</i>	<i>Atta colombica tonsipes</i>	predator	Weber, 1941
Squamata	<i>Basiliscus basiliscus</i>	<i>Sericomyrmex amabilis</i>	predator	Barden, 1943
Squamata	<i>Coecilia annulata</i>	<i>Atta cephalotes</i>	in nest	Schomburgk, 1844
Boidae	<i>Elapomorphus lemniscatus</i>	<i>Acromyrmex lobicornis</i>	in nest	Weber, unpubl.
Caprimulgiformes	<i>Chordeiles minor</i>	<i>Atta texana</i>	predator	Walter <i>et al.</i> , 1962
Galliformes	domestic fowl	<i>Acromyrmex octospinosus</i>	predator	Weber, 1947
Edentata	<i>Tamandua longicauda</i>	<i>Acromyrmex octospinosus</i>	predator	Weber, 1945
Edentata	<i>Tamandua longicauda</i>	<i>Atta cephalotes</i>	predator	Weber, 1945

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